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AN INVESTIGATION OF THE DISTRIBUTION OF THE MAYFLY FAUNA OF A LANCASHIRE STREAM

BY JANET E. HARKER

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(With 3 Figures in the Text)

This investigation was designed to study in detail the movements and variation in numbers of the mayfly fauna of a small section of a stream.

The stream chosen was Broadhead Brook at Entwistle, Lancashire (Fig. 1), which runs from its source at an altitude of 900 ft. to Wayoh Reservoir (550 ft.), a distance of about two miles. The surrounding country is agricultural farm land, except for the first half mile where moorland conditions still exist. In the lower reaches of the stream artificial falls have been built to prevent undue damage when flooding occurs. The width of the stream is fairly constant at about 30 ft., but the whole stream bed is very seldom covered. The bed is stony, or in places sandy, with little mud; and the main flow is such as to prevent blockage with leaves.

The stream is a fast filling one, and during the September floods of 1950 the whole bed of the stream changed its form; the artificial falls were in many places completely dislodged, and the large concrete slabs so displaced blocked the flow, causing a new course to be taken.

The area of the stream selected for detailed work was bounded at the upper end by an artificial fall, and at the lower by an incline leading to a second fall. This region of the stream was fairly straight and could be easily marked off into a number of stations by a series of parallel lines. The stream was divided longitudinally into ten regions, each 3 ft. apart, and transversely into fourteen regions, chosen so as to include various habitats and to keep one type of habitat only within each station. One hundred and forty stations were thus marked, covering approximately 30×150 sq. ft.

In May 1950 the mayfly fauna of the stream completely disappeared in this area. The disappearance seemed to be associated in some way with an extraordinary increase in the number of blue-green algae and diatoms, which practically blocked the stream at that point. Large numbers of dead nymphs were found under the algae, but whether they were killed by some toxic product, a lack of oxygen (there was no fall in the daytime oxygen content) or perhaps an increase in temperature is not known. Mayflies were still abundant in a region just below the experimental area where no increase in the amount of algae occurred.

The original stream was still kept under observation, but when the nymphs disappeared another stream was included in the survey. This stream, Wayoh Stream, joins Broadhead Brook nearly a quarter of a mile below the experimental area, and at the chosen area runs parallel to it. The two are separated by a small rise, and are about 500 yards apart, but there is no connexion between them until they finally unite. A similar area to the original experimental area was selected and divided in like manner

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into a number of stations by longitudinal and transverse lines, giving 100 stations in all.

Wayoh Stream is narrower than Broadhead Brook, and the marked stations covered an area of approximately 15 × 200 sq. ft. The stream bed is stonier than that of Broadhead Brook, and the banks are wooded.

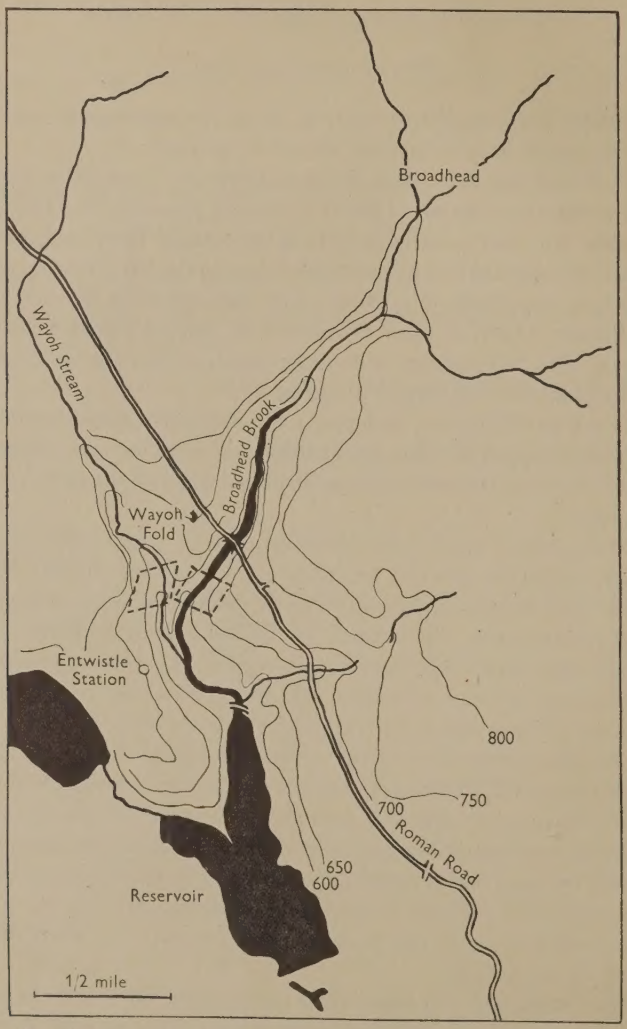

Fig. 1. Map showing the positions of the areas investigated, marked by dotted lines.

The fauna of both streams consists of fairly typical brook forms such as Planarians *Dendrocoelum*, *Hydropsyche*, *Rhyacophila*, *Simulium*, *Cottus*, etc.

During the period September 1949 to August 1951 a sample of the mayfly fauna was taken at each station at regular monthly intervals. In addition to this, measurements

of the current-rate, temperature, concentration of dissolved oxygen, and the depth were made at each station.

PHYSICAL AND CHEMICAL CHARACTERISTICS

(*a*) *Current*

A simple right-angled pitot tube (Dodds & Hisaw 1924) was used to measure the current. The main disadvantage of the method was the necessity of taking readings of the water-level at the surface of the stream. In turbulent water this became almost impossible, but the difficulty was partly overcome by surrounding the pitot tube at the stream water-level by a glass tube of larger diameter, and thus eliminating the ripples. The slowest movement which could be measured was 0·15 m./sec. Measurements were made at the surface of the stream as the water was in parts too deep for readings at the bottom to be taken.

The maximum and minimum current-rates for each month are given in Table 1. Throughout the year the average rate of flow varied from 0·1 to 2·5 m./sec. or from

Table 1. *The physical and chemical conditions each month in Broadhead Brook* (B) *and Wayoh Stream* (S)

	Average depth (cm.)		Current (m./sec.) Max.		Current (m./sec.) Min.		pH		Average dissolved oxygen (% sat.)		Average temperature (° C.)	
	B	S	B	B	S	B	S	B	S	B	S
13 Sept. 1949	8	—	1·5	0	—	7·4	—	—	—	13	—
11 Oct.	43	—	0·9	0	—	7·4	—	—	—	13	—
8 Nov.	43	—	0·9	0	—	7·4	—	99	—	13	—
2 Dec.	27	—	2·0	0	—	7·6	—	70	—	4	—
12 Jan. 1950	32	—	1·3	0	—	7·8	—	60	—	2·5	—
13 Feb.	49	—	0·5	0	—	7·4	—	76	—	2·5	—
10 Mar.	18	—	0·5	0·1	—	7·4	—	74	—	6	—
8 Apr.	28	—	0·3	0·1	—	7·4	—	75	—	8	—
9 May	—	31	—	—	0·1	—	7·4	—	101	—	15
8 June	—	27	—	—	0·1	—	7·5	—	97	—	11
5 July	—	32	—	—	0·1	—	7·6	—	112	—	14
14 Aug.	—	28	—	—	0·3	—	7·4	—	114	—	15
11 Sept.	—	31	—	—	0·1	—	7·5	—	100	—	12
6 Oct.	10	53	3·0	1·6	0·6	7·5	7·5	92	90	8	8
2 Nov.	48	16	2·0	1·3	0·2	7·5	7·5	74	79	4	4
6 Dec.	48	23	1·5	0	0·1	7·5	7·5	69	66	2	2
14 Jan. 1951	33	22	1·4	0·1	0·1	7·5	7·4	63	65	2	2
1 Feb.	14	17	0·9	0·2	0·2	7·4	7·4	77	79	5	5
1 Mar.	16	19	1·0	0·2	0·2	7·4	7·4	74	76	7	7
2 Apr.	16	20	0·9	0·1	0·1	7·4	7·4	75	78	7	7
1 May	15	19	0·8	0	0·1	7·4	7·4	69	72	12	12
2 June	17	18	1·0	0·1	0·1	7·4	7·4	93	104	11	11
1 July	19	23	0·7	0·1	0·1	7·4	7·4	79	82	10	10
1 Aug.	16	20	0·4	0	0	7·5	7·4	74	76	10	9

a very slow current to a very strong current. During some months of the year the same range could be found within the stream at any one time; for instance in September 1950 the rate varied from 0·1 to 2·5 m./sec., in December from 0 to 2·0 m./sec. But in some months the readings showed very little variation anywhere, for example from March to July the fastest current was 0·4 m./sec. The regions of greatest velocity altered throughout the year, particularly after the January and October floods.

(*b*) *Depth*

The depth of the water was measured monthly at each station. Particularly in Broadhead Brook, it varied markedly from month to month, so that from one month to the next the two extremes of depth found within the stream may appear in the one station. Fig. 2 and Table 1 show the depth and rate of flow of the water in both streams

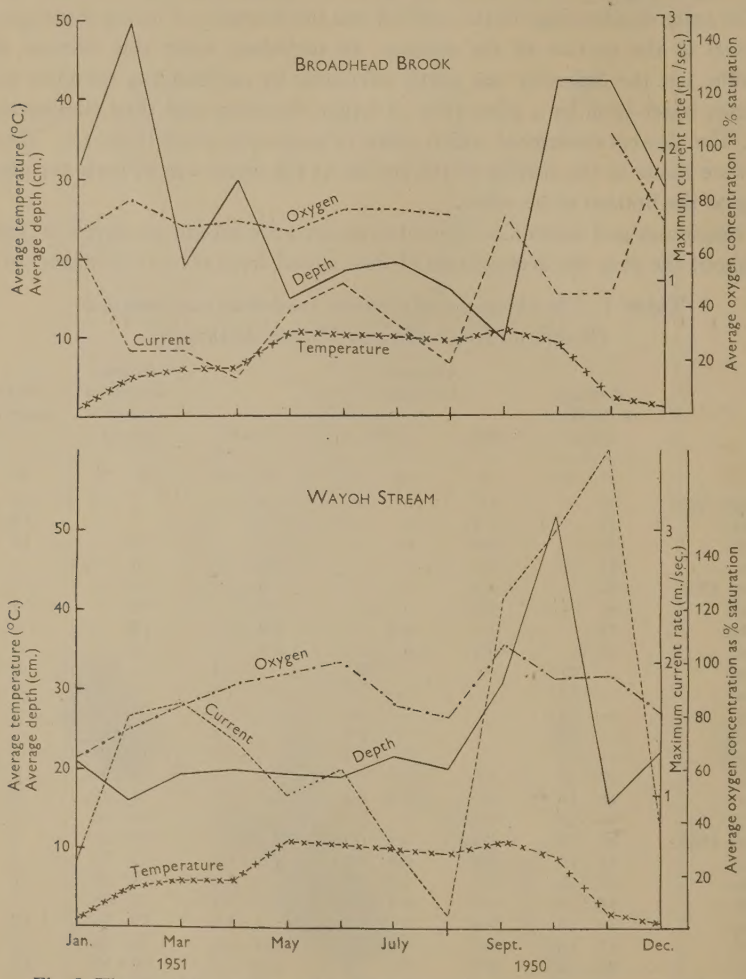

Fig. 2. The monthly maximum flow, average depth, oxygen concentration, and temperature in Broadhead Brook and Wayoh Stream.

over 12 months. The years have not been shown in order because of the break in readings in Broadhead Brook, but even so the picture given may be assumed to show approximately the conditions over a year.

In Broadhead Brook there is an almost complete inverse correlation between depth and speed, obvious in particular in December, January, April and September. The

rate of flow will depend on the quantity of water coming downstream, the drainage below the experimental area, and the width of the stream. In September there is an increase in the rate of flow due to the autumn rains, but the water at first drains away quickly, so that there is no increase in depth. Later, flow is less rapid because the drainage from the surrounding areas into the lower reaches increases, causing the level to rise and the flow to slacken. During the summer months the stream has been flowing through a narrow channel, giving in April and May a relatively fast rate of flow, but after the autumn rain the water flows through the whole channel causing again a decrease in depth. In February the snow begins to melt and causes another increase in depth, but probably because of the slow rate of the process there is little effect on the speed.

Wayoh Stream is narrower and on more of a slope, so that a slightly different relationship is found between the depth and flow. There appears to be what might be termed a basic depth at which the water can run off quite fast, and yet fluctuations about this depth do not directly affect the current-rate. In general, in this stream a decrease in speed only occurs at the beginning of an increase in depth, and then the depth builds up to a point where the water runs away fast.

(*c*) *Dissolved oxygen*

The dissolved oxygen concentration of the water was measured by the Winkler method, using a portable apparatus (Whitney 1938). The percentage saturation of the water has been calculated from Ricker's nomogram (1934). The average saturation varied between 60 and 114% during the 24 months, so that even when the stream was frozen the concentration was not very low. An oxygen gradient occurred during the summer months between some of the stations. Beneath the fall at the upper end of Broadhead Brook supersaturation to the extent of 114% saturation was measured. Although this appears to be a very high reading, water from this region, when kept at constant temperature, retained this degree of supersaturation for some hours. When few algae were present at the side of the stream the concentration fell to 58% saturation if the temperature was high.

(*d*) *Temperature*

The annual range in temperature is about 18° C., as measured by the monthly readings. The edges of the stream froze from December 1949 to March 1950, and all but a stream about 10 in. wide froze in January 1950 when the ice near the banks was 3 in. thick. In December 1950 and January 1951 the whole stream froze over, but the water was flowing quite freely underneath the ice in the central part of the stream.

A temperature gradient was present across the stream during the summer months when the temperature of the shallow side regions often rose to 20° C., as compared with 11–14° C. in the central region. No vertical temperature gradient was present.

(*e*) *Chemical properties*

The hydrogen-ion concentration of the water was measured each month colorimetrically. The pH was found to range from 7·4 to 7·8 from September 1949 to February 1951.

As the fields which were under cultivation near part of Broadhead Brook were limed during the year, calcium determinations were made to ascertain whether the lime was being washed into the stream. The calcium content did not vary to any appreciable extent over the year, and was very low, averaging 1·0 p.p.m.

THE DISTRIBUTION OF THE FAUNA

(*a*) *Sampling technique*

Samples were obtained of the fauna at each station using the following method. A galvanized iron square, enclosing an area of 530 sq.cm. was plunged into the water and pushed well down into the stream bed. The stones within the area were turned over, and the number of nymphs present was counted. Most nymphs were found clinging to the bottom of larger stones; these stones were removed with the nymphs still attached, and piled carefully outside the square, later to be replaced. The nymphs which were washed off or free swimming, were caught in a very small hand-net and held there until the counting was finished. All the nymphs were replaced, and the stones as nearly as possible returned to their original positions.

There are at least two obvious sources of error involved in this method. Possible numbers of nymphs were either overlooked or counted twice, and each count involved disturbance of the habitat. Any method of sampling the population of a fauna living mainly beneath stones must of necessity involve the disturbance of the habitat; the method had, of all the methods tried, the least effect on the habitat. Also each station was at least 3 sq.yd. in area, so that a period of 4–5 months elapsed between sampling of exactly the same position. It may be objected that the sampling of slightly different areas each month is another source of error. It will be remembered that each station consisted, as far as possible, of only one type of habitat, and preliminary counts showed that the numbers from any area within each of the stations were very similar. These preliminary counts were compared with results obtained from other sampling methods; collecting for a definite period of time in each area, and in another part of the stream dredging the bottom and sorting the material in the laboratory. While these methods are not suitable for the type of work which was being done, they served as a check on the standard method used, and showed that very little double counting or omission of the nymphs can have taken place. When the water was very deep and the current fast there may have been more nymphs washed away; when the nymphs were more numerous there may have been some double counting. These errors emphasize the scarcity or abundance, as the case may be, but should give a fairly accurate picture.

After each count a sample of the nymphs of each of the species counted was retained and further examined in the laboratory to check the identifications. The four species counted were *Ecdyonurus torrentis* Kimm., *Heptagenia lateralis* (Curt.), *Rithrogena semicolorata* (Curt.) and *Baëtis rhodani* (Pict.). The only other nymphs found in the stream were *Ephemerella* and *Paraleptophlebia*, neither of which was likely to be confused with the ones under observation. No other species of the four observed genera was present, and each could be easily distinguished from the others by the body shape, markings, and the type of movement.

(*b*) *Seasonal variations*

Ecdyonurus torrentis. Two sizes of nymph were recognized in this species, as they appeared to be separately distributed. Large nymphs were those with fully developed gills, with the metathoracic pair of wing pads completely hidden by the mesothoracic pair, and the lateral margins of the wing pads sloping inwards (stages XIV–XVII of Rawlinson 1939). Small nymphs were those which did not fall into the large class and consisted of those nymphs without gill pads (stages IX–XIV of Rawlinson). Stages smaller than this, that is less than about 3 mm., were too small to be counted. The results are expressed as the average number of nymphs per station, which gives an appearance of very few nymphs per count as there were frequently no nymphs at all present in some of the very deep stations. The results of the counts are shown in Fig. 3 and Table 2.

E. torrentis disappeared completely in Broadhead Brook during May 1950 when the previously described algal growth occurred, and no trace of re-establishment was found.

The life-cycle of this species as it occurs in this stream has been described elsewhere (Harker 1952). Three broods develop, approximately in March–July, July–May and May–March. Nymphs of two different broods are thus always present in the stream at any one time. The increase in numbers of large nymphs from February to June 1950 is due to the growth of the overwintering nymphs. In February and March the May–March brood nymphs were nearing their full size, and in April and May the July–May brood were reaching their penultimate instar. By July all the nymphs from the March–July brood had emerged as adults. Therefore only small nymphs were left, except for a few nymphs from the May-March brood which entered the larger group in August, causing the increase in that month. Other increases caused by the growth during the summer will be masked by emergence of some nymphs as adults, so that the total population of large nymphs does not alter appreciably. Decreases in the number of large nymphs were seen to occur in November 1949 and 1950, and in July 1950. The decreases in November 1949–50 appear to be due to migration upstream; the reasons for this supposition will be discussed in a later paper. The decrease in July 1950 can be explained on the basis of the emergence of the adults of the March–July brood which left only the small nymphs which hatched in May.

Apart from the major increases and decreases caused by the life-cycles of the nymphs there are those caused by the environment. Flooding of the stream was a factor which appeared to have a marked effect on *E. torrentis*. Evidence for this was gained rather by an examination of the stream than by the counted number of nymphs. This is due to the difficulty in separating the decreases in number due to the life-cycle from those resulting from the environment. After a flood crushed nymphs were invariably found in any drift, and the very fact that nymphs were previously found associated with stones which were swept away or ground together supports this evidence. In December 1949 the stream flooded slightly. The numbers did not decrease appreciably, but this may be due to the fact that very few nymphs were present anyway. Two other minor floods occurred in August and September 1950. Although the numbers had increased in August, it may be supposed that they had not in fact increased as much as

they would have done had the flood not occurred. The slight decrease in numbers in September supports this supposition, and increase in numbers would be expected in September as the nymphs hatching in July would then be appearing in the larger

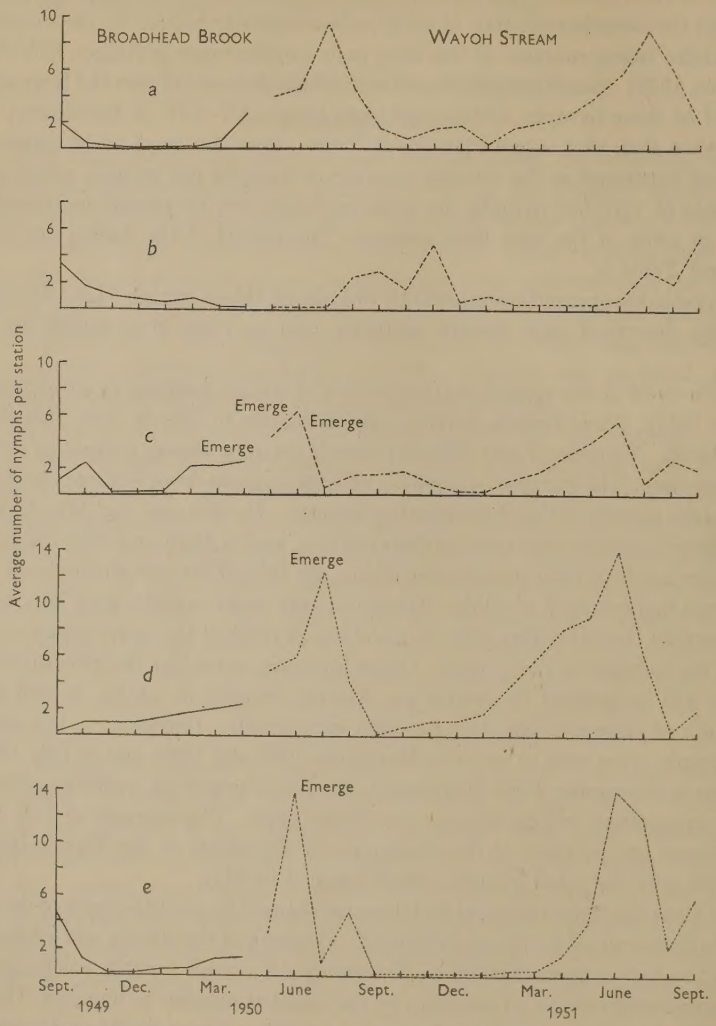

Fig. 3. The monthly average number of nymphs collected in a 530 sq.cm. area at 140 stations in Broadhead Brook and 100 stations in Wayoh Stream. (*a*) *Baëtis rhodani*; (*b*) *Ecdyonurus torrentis*, small nymphs; (*c*) *E. torrentis*, large nymphs; (*d*) *Rithrogena semicolorata*; (*e*) *Heptagenia lateralis*.

classes in which they overwinter. In August 1951, when no flooding occurred, a much greater increase in numbers is shown. The bad flood in October 1950 does not seem to have affected the nymphs any more than the smaller floods. Probably all the nymphs attached to small rocks had by that time already been swept away, or had moved to more secure stones which had not been moved by the flood waters.

The slow decrease in numbers of small *E. torrentis* nymphs from September 1949 to February 1950 may be due to gradual growth during the winter causing nymphs to enter the 'large' class at this time. The sudden decrease in March coincides with a period of rapid growth taking many nymphs into the larger class. The nymphs hatching out in March do not appear in great numbers, probably because the increase in numbers is masked by the decrease of small nymphs at the upper size level. But the nymphs hatching in July, and some of the later May brood, both appear in August counts, causing a sudden increase in numbers. The increase in February 1950 and 1951 is again thought to be related to migration.

Table 2. *Monthly collections*

(The figures give the average number of nymphs per station collected each month followed by the standard deviation.)

	Heptagenia lateralis	*Ecdyonurus torrentis* (large)	*Ecdyonurus torrentis* (small)	*Baëtis rhodani*	*Rithrogena semicolorata*
BROADHEAD BROOK					
Sept. 1949	10·2 ± 3·1	1·1 ± 0·3	3·3 ± 0·7	1·8 ± 0·07	0·4 ± 0·03
Oct.	1·3 ± 0·2	2·3 ± 0·4	1·9 ± 0·8	0·5 ± 0·05	1·0 ± 0·02
Nov.	1·3 ± 0·1	0·1 ± 0·01	0·9 ± 0·01	0·3 ± 0·03	1·0 ± 0·02
Dec.	0·1 ± 0·01	0·1 ± 0·01	0·8 ± 0·04	0·4 ± 0·02	1·0 ± 0·03
Jan. 1950	0·3 ± 0·1	0·3 ± 0·02	0·6 ± 0·07	0·1 ± 0·01	1·3 ± 0·07
Feb.	0·5 ± 0·2	2·0 ± 0·1	0·8 ± 0·06	0·1 ± 0·01	1·8 ± 0·9
Mar.	1·4 ± 0·1	2·1 ± 0·9	0·2 ± 0·02	0·5 ± 0·02	2·1 ± 0·8
Apr.	1·5 ± 0·3	2·6 ± 0·5	0·1 ± 0·03	2·8 ± 0·02	2·3 ± 0·8
WAYOH STREAM					
May	3·2 ± 0·5	4·5 ± 1·0	0·1 ± 0·03	4·1 ± 0·09	5·0 ± 1·1
June	12·8 ± 1·3	6·3 ± 0·9	0·08 ± 0·05	4·6 ± 0·2	6·0 ± 0·1
July	1·1 ± 0·2	0·6 ± 0·1	0·08 ± 0·07	9·7 ± 0·3	12·5 ± 0·5
Aug.	5·0 ± 0·3	1·6 ± 0·2	2·5 ± 0·09	4·5 ± 0·02	3·9 ± 0·6
Sept.	0·3 ± 0·1	1·5 ± 0·1	2·8 ± 1·01	1·6 ± 0·3	0·2 ± 0·01
Oct.	0·2 ± 0·01	1·9 ± 0·2	1·5 ± 0·9	1·0 ± 0·9	0·9 ± 0·07
Nov.	0·2 ± 0·01	0·8 ± 0·01	4·7 ± 0·8	1·6 ± 0·7	1·0 ± 0·02
Dec.	0·2 ± 0·01	0·3 ± 0·03	0·6 ± 0·04	1·7 ± 0·6	1·2 ± 0·09
Jan. 1951	0·3 ± 0·01	0·2 ± 0·05	0·9 ± 0·02	0·3 ± 0·02	1·7 ± 0·08
Feb.	0·4 ± 0·02	1·3 ± 0·3	0·4 ± 0·03	1·6 ± 0·03	3·8 ± 0·1
Mar.	0·5 ± 0·05	1·9 ± 0·1	0·4 ± 0·02	2·0 ± 0·9	5·9 ± 0·2
Apr.	1·6 ± 0·09	3·0 ± 0·4	0·4 ± 0·02	2·6 ± 0·9	8·0 ± 2·0
May	4·0 ± 0·8	4·1 ± 0·9	0·5 ± 0·03	3·9 ± 0·2	9·1 ± 1·1
June	14·0 ± 2·1	5·6 ± 1·1	0·8 ± 0·08	5·8 ± 0·9	13·9 ± 1·9
July	12·1 ± 2·4	1·0 ± 0·07	2·9 ± 0·1	9·0 ± 1·3	6·0 ± 1·0
Aug.	2·2 ± 1·0	2·8 ± 0·09	2·0 ± 0·2	6·0 ± 1·8	0·6 ± 0·03
Sept.	5·9 ± 0·8	2·0 ± 0·07	5·4 ± 0·2	2·1 ± 0·9	2·0 ± 0·2

Flooding does not seem to have affected the small nymphs as much as the larger ones. The dead nymphs found at these times were very seldom of the small nymph class. The major flood in October 1950 coincided with a natural decrease in numbers as can be seen by reference to the figures for the same month in 1949. Freezing of the stream may have affected *E. torrentis* slightly, as the numbers in December 1950 and January 1951, when the stream was frozen, decreased slightly more than in the same months of the previous year.

Rithrogena semicolorata. Owing to the limitations imposed by the inability of the observer to count more than a certain number of nymphs during any one counting

period, the nymphs of this species were treated as a whole and not divided into small and large nymphs. Preliminary counts showed no distinctive distribution in August and September of the small and large nymphs, as was found for those of *Ecdyonurus torrentis*. The results of the monthly counts are shown in Fig. 3.

Rithrogena semicolorata was one of the two species which returned to Broadhead Brook after the algal growth in May 1950. In October 1950 an average number of 0·08 nymph per station was found and this number increased to 2·2 by February 1951. Since the new appearance in October coincides with the hatching of eggs in Wayoh Stream it seems likely that the two nymphs in Broadhead Brook are the offspring of adults emerging from Wayoh in August 1950. The slow increase in numbers from October to March is probably due to the gradual growth of nymphs from eggs hatched in May, June and July, which are reaching a countable size. The increase to 6·5 nymphs per station in July corresponds with the period shown in the life cycle when the nymphs from the June hatching become large enough to count, and before the occurrence of the major emergence in July itself. The drop in numbers in August coincides with the end of the emergence period and is a common feature in 1-year life cycles.

Flood has affected *R. semicolorata* less than any other species. Again this is concluded rather from observation than from the numbers counted. No crushed *Rithrogena* nymphs were collected after floods, and the sucker-like arrangement of the gills gives a greater adhesive power than is found in other species (Harker 1951). A decrease in numbers occurred in August and September 1950 coinciding with floods, but also coinciding with the annual emergence which must cause a decrease in numbers. In October 1950 when the worst flood occurred the number actually increased, and in December 1949 after a flood no decrease in numbers was found. Freezing of the stream did not affect the numbers of nymphs. The stream was frozen in December 1950 and January 1951 and yet the numbers increased more than they did in the same months of the previous year.

Heptagenia lateralis. The results of the monthly counts are given in Fig. 3. The main emergence in June would account for the drop in numbers in July and the following increase in August, as the nymphs hatching from the eggs laid in June began to enter the counts.

H. lateralis lives in very similar habitats to those of *Ecdyonurus torrentis*. The main peaks in the totals of *E. torrentis* occur in June and October, while a peak appears in the numbers of *Heptagenia* in June, August or September. Floods affected *H. lateralis* more than any other species, the numbers dropping after every flood. The very low numbers in Broadhead Brook may be associated with the unstable bottom as compared with that of Wayoh Stream

Baëtis rhodani. The nymphs of this species are often found on the tops of stones and swimming freely in the water, so that it was the most difficult species to count, and the results (Fig. 3) are probably less accurate than for those of other species. The numbers for the total population do not indicate the complexity of the life cycle, nor the presence of the two different sizes of nymphs (Harker 1952).

B. rhodani reappeared in Broadhead Brook in November 1950, an average of 0·2 nymph per station being present. This number increased to 1·1 per station by February 1951. Although no separate counts of small and large nymphs were made

it was noted that the very small nymphs, which do not appear in the counts, were present in the water just below the overhanging grasses and weeds at the edges of the deeper parts of the stream.

B. rhodani was only slightly more affected by floods than *Rithrogena*. Again the totals were dropping owing to emergence at the times of the floods, and the numbers do not indicate the resistance of these nymphs to fast-flowing currents.

(*c*) *Micro-distribution*

The nymphs of each species were found to follow a Poisson distribution over the experimental area in the following months: *R. semicolorata* December 1950, January and February 1951; *Ecdyonurus torrentis*, small nymphs, and *Baëtis rhodani*, August, September and October 1950, *Ecdyonurus torrentis*, large nymphs, February 1951; *Heptagenia lateralis* July 1950. In other months between September 1949 and February 1951 distribution was not random. Some difficulty has been experienced in relating the counts at each station to the depth or current since the total number of nymphs, the frequency of each type of habitat, and the total number of habitats actually covered by the stream varied each month. Using Spearman's rank correlation coefficient no significant correlation has been found between the depth at each station and the number of nymphs. However, correlating the relative depths (in groupings of 25% of the greatest depths) with the number of nymphs, using the same coefficient, shows a significant correlation at the 1% level in some months, Bessel's correction having been applied for the small sample size (Table 3). That is, the nymphs in general do not show a distribution correlated with absolute depth, but are associated with the relative degrees of depth.

Ecdyonurus torrentis large nymphs showed a correlation at the 5% level in December 1950 and January 1950–51, with the greatest number in depths above 75% of the deepest area. From March to August 1950 the correlation was at the 1% level with the majority of nymphs in the 0–25% depth area. No correlation was found between the relative depths and the number of small *E. torrentis* nymphs. The number of *Baëtis rhodani* nymphs showed a direct correlation with the relative depths at the 1% level in autumn from September to December 1949 and 1950. There was no significant correlation in other months of the year. *Heptagenia lateralis* nymphs were in the majority in the shallow areas from December to March and showed a significant correlation with the relative depth at the 1% level. In summer the correlation was significant at the 5% level, with the greatest number of nymphs in the shallow areas. The number of nymphs of *Rithrogena semicolorata* shows a correlation at the 1% level with the relative depth from June to August when the nymphs were in depths above 75% of the deepest area.

The number of nymphs was found to be correlated with the current-rate, using the rank correlation, in the same months in which a correlation was shown between depths and numbers. The current-rates were taken at the surface of the stream, and the current at the bottom will be related to the depth; it is impossible to separate the two factors in considering the micro-distribution of the nymphs.

From the results it appears that the nymphs of *Ecdyonurus torrentis* and *Heptagenia lateralis* are present in the shallow regions during the emergence periods, but *Rithro-*

gena semicolorata is in the deeper areas during this period. *Baëtis rhodani*, which emerges from the top of the water without crawling up a stone, is randomly distributed when emergence is at a maximum. The movement of nymphs of *B. rhodani*, *Heptagenia lateralis* and *Ecdyonurus torrentis* into shallow water seems to be associated with the floods. Whether this is actually movement to the shallow parts or whether the relative numbers are lowered in the deeper parts by nymphs being swept away is not known.

Table 3. *Correlation of relative depths, in ranks of 25% of the total depth, with the number of nymphs*

(S = level of *t*-value (%). D = the relative depth at which the majority of nymphs were found.)

	Ecdyonurus torrentis (large)		*Heptagenia lateralis*		*Rithrogena semicolorata*		*Baëtis rhodani*	
	S	D	S	D	S	D	S	D
Sept. 1949	0	—	5	25	0	—	1	75
Oct.	0	—	0	—	0	—	1	75
Nov.	0	—	0	—	0	—	1	75
Dec.	5	75	1	25	0	—	1	75
Jan. 1950	5	75	1	25	0	—	0	—
Feb.	5	75	1	25	0	—	0	—
Mar.	1	25	1	25	0	—	0	—
Apr.	1	25	0	—	0	—	0	—
May	1	25	0	—	0	—	0	—
June	1	25	0	—	1	75	0	—
July	1	25	5	25	1	75	0	—
Aug.	1	25	5	25	1	75	0	—
Sept.	0	—	5	25	0	—	1	75
Oct.	0	—	0	—	0	—	1	75
Nov.	0	—	0	—	0	—	1	75
Dec.	5	75	1	25	0	—	1	75
Jan. 1951	1	75	1	25	0	—	1	75
Feb.	5	75	1	25	0	—	0	—
Mar.	1	25	1	25	0	—	0	—
Apr.	1	25	1	25	0	—	0	—
May	1	25	0	—	0	—	0	—
June	1	25	0	—	1	75	0	—
July	1	25	1	25	1	75	0	—
Aug.	1	25	5	25	1	75	0	—

It has been shown for every species that distribution is neither random, nor correlated with the depth or current in some months of the year. These months are as follows: *E. torrentis*, large nymphs, September, October, November; *Baëtis rhodani*, January to May; *Heptagenia lateralis*, April to June, October to December; *Rithrogena semicolorata*, March to June, September to December. What factors are influencing the distribution at these times is not apparent.

ACKNOWLEDGEMENTS

This work was carried out while the author was the holder of the Grisedale Research Scholarship and the Philip Buckle Studentship of Manchester University.

SUMMARY

1. The numbers of nymphs of *Ecdyonurus torrentis*, *Heptagenia lateralis*, *Baëtis rhodani*, and *Rithrogena semicolorata* in a 530 sq.cm. area at each of 140 stations in Broadhead Brook and 100 stations in Wayoh Stream, Lancashire, were counted every month from September 1949 to August 1951.

2. At each station the current and depth were measured. The temperature, pH, calcium concentration and oxygen concentration were measured at various points.

3. The seasonal variations in the numbers of *Ecdyonurus torrentis* followed the course of the life-cycle and were also affected by flood. Freezing of the stream caused a decrease in numbers. The numbers of *Rithrogena semicolorata* followed the life-cycle closely. *Heptagenia lateralis* was found to be very much affected by floods. *Baëtis rhodani* was little affected by floods, and together with *Rithrogena semicolorata* repopulated Broadhead Brook after the fauna had disappeared during an excessive growth of algae.

4. *Ecdyonurus torrentis* and *Heptagenia lateralis* moved to shallow regions at the emergence periods and during floods. *Rithrogena semicolorata* moved to deeper water at the time of emergence. *Baëtis rhodani* is randomly distributed most of the year.

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THE RELATIVE ABUNDANCE OF DIFFERENT SPECIES IN A WILD ANIMAL POPULATION

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(With 9 Figures in the Text)

In a series of papers published during the past six years I have discussed the frequency distribution of the relative abundance of different species of animals in random samples from wild populations.

From data obtained, chiefly by collecting Lepidoptera in a light-trap, it was found that there was an orderly distribution in such samples, and in practically all cases the number of species represented by one individual was greater than the number represented by two, the number with two greater than that with three, and so on. The distribution in the sample, on an arithmetic scale of number of individuals per species, was in the form of a 'hollow curve'.

Many different mathematical formulae can be represented graphically by curves of this type, and it is unfortunately often difficult to distinguish between them, especially with variable biological data. This difficulty is greater in small samples, but less in large samples.

It was found that the logarithmic series (which is a special form of the negative binomial) gave a very good fit to the data obtained from most of our trapping experiments, and also to evidence from other sources. This series has the form

$$\alpha x;\quad \alpha x^2/2;\quad \alpha x^3/3;\quad \alpha x^4/4;\quad \text{etc.};$$

where the successive terms are the number of species represented by 1, 2, 3, 4, etc. individuals. The x is a number less than unity which is constant for any one sample from a population; but it varies according to the size of the sample, being larger in large samples and gradually approaching unity in very large samples. The α, on the other hand, is a constant for all samples from the same population; it is a property of the population and not of the sample, and we have called it the 'Index of Diversity' (Fisher, Corbet & Williams 1943).

Since the number of species represented by one individual each is αx it follows that, with increasing size of sample, this must increase as x increases until in large samples it approaches very close to α. Thus, in populations with a frequency distribution based on the log-series, α is not only a measure of diversity, but is also the upper limit to the theoretical number of species which can be represented by one individual either in a very large sample or in the population itself.

There is no doubt that the log-series has given a very close fit to observed data in many samples of animal populations, and that many deductions from it, such as the straight-line relation between number of species and the logarithm of the number of individuals in samples of different sizes, have also been found to be correct within the

limit of normal sampling. Normal samples, however, usually consist of a few thousand individuals, or perhaps occasionally a few hundred thousand, while populations, at least in insects, have to be reckoned in millions; so there is always considerable extrapolation necessary in arguing from the structure of a sample to the structure of the population.

Theoretically the log-series is one in which the form of the series is not altered by the process of sampling. If a population is arranged in a log-series, then any random sample from it is also in the form of a log-series with the same α but a lower value of x. Thus if any sample was a mathematically exact fit to log-series, we would be correct in inferring a similar distribution in the population sampled. This mathematical exactitude is, however, just what can never be obtained in biological observations.

In 1948 F. W. Preston suggested that the frequency distribution of an animal population might be a log-normal distribution, and not a logarithmic series. This distribution (which is a continuous curve and not a discontinuous integer series) is the normal Gaussian curve when the dimensions of the variate are expressed in logarithmic classes instead of on an arithmetic scale. Preston further suggested that the frequency distribution found in a small sample from a population arranged in a log-normal pattern is a 'truncate log-normal', and that this, when shown on an arithmetic scale, may very closely resemble a logarithmic series distribution.

It is therefore of considerable interest to see how these two alternative suggestions can be separated, if the biological data at our disposal are sufficiently accurate to support one or the other, and what are the implications of accepting either one or the other. There remains, of course, always the likelihood that neither is the really correct solution.

In the first place attention should be drawn to the fact that the log-normal distribution has three constants or parameters, while the logarithmic series has only two. In the case therefore of data that are a possible fit to either, the curve with three constants would automatically give a better fit to the data without explaining more. For a given number of individuals and a given number of species, there is only one possible log-series, but many log-normals. A logarithmic series is defined by the total number of individuals and the total number of species, but to define a log-normal curve a third quantity is necessary—one involving the 'standard deviation' of the distribution. The form of the log-normal curve is determined by the total number of species (the area of the curve) and by the standard deviation: the position of its median is determined by the number of individuals.

It has already been pointed out that, if in the logarithmic distribution a series of samples of increasing size is taken from the same population, the number of species with one individual (n_1) is equal to αx; it is small with very small samples, increases rapidly at first, and then more and more slowly till it approaches to the value of α. It cannot, except by chance error, surpass this value, nor does it theoretically show any fall as the sample size is further increased so as to include the whole population.

In the case of the log-normal population, the number of species represented by one individual will start small in small samples, rise at first rapidly, then more slowly, as sample size increases, till it reaches a peak when the sample is of such a size that about half the species in the population have been obtained; after this the number will

fall at first slowly, then more rapidly and finally very slowly again, till it becomes very small in the whole population.

A second difference is that with the logarithmic series the number of species represented in a series of samples of increasing size is, except in small samples, always proportional to the logarithm of the size of the sample; i.e. there is graphically a straight-line relation between the number of species and the logarithm of the number of individuals. With the log-normal the number of species in samples of increasing size at first increases slowly, then takes up a straight-line relation very similar to the logarithmic series, but in larger samples, when over half of all the species in the population are represented, the rate of increase of species falls off so that the curve for the relation

Table 1. *Number of species of Macro-lepidoptera with different numbers of individuals, caught in a light trap at Harpenden in the year 1935*

(Total catch = 6814 individuals representing 197 species; an average of 34·6 individuals per species. On the assumption of the log series $x = 0{\cdot}994$, $\alpha = 38$.)

On arithmetic scale

Individuals	Species	Individuals	Species	Individuals	Species	Individuals	Species
1	37	11	2	21	4	31	—
2	22	12	4	22	1	32	—
3	12	13	2	23	1	33	2
4	12	14	3	24	—	34	2
5	11	15	2	25	1	35	—
6	11	16	2	26	—	36	—
7	6	17	4	27	—	37	—
8	4	18	2	28	2	38	1
9	3	19	—	29	2	39	1
10	5	20	4	30	—	40	3

and also at 42(2), 48(2), 51, 52, 53, 58, 61, 64(2), 69, 73, 75, 83, 87, 88, 105, 115, 131, 139, 173, 200, 223, 232, 294, 323, 603 and 1799

In geometric ×3 classes

I	II	III	IV	V	VI	VII	VIII
37	46	48	37	19	8	1	1

between number of species and log-number of individuals is sigmoid. It would be necessary, however, to have a sample large enough to contain at least 80% and perhaps 90% of the species in the population before the sigmoid nature of the curve would be obvious graphically.

To differentiate between the two alternative theories by either of these methods, a series of samples of different sizes must be obtained, and the larger samples must be taken under conditions which are identical with those of the smaller samples. This is not always practical. A third, more promising, method of distinction is a study of the form of frequency distribution within a sample when the numbers of individuals per species are grouped together in classes on a geometrical scale instead of in an arithmetic scale. To do this Preston made what he called a series of 'octaves', each class being twice the size of the previous, by adding all species with from 1 to 2 individuals in octave I, 2 to 4 individuals in octave II, 4 to 8 individuals in octave III, 8 to 16 individuals in octave IV, etc.

This system, however, necessitated splitting the numbers of species with 1, 2, 4, 8, etc., individuals into those below the integer, which go into the lower class, and those above the integer which go into the higher. The word 'octave' is also unfortunate as

its derivation and general use in music is based on the eight notes into which each octave is divided, and not on the fact that the frequency of vibration is doubled.

If instead of this series we define the first class to include all values between 0·5 and 1·5, and (since 1·5 is 3 times 0·5) the second class all values between 1·5 and 4·5, and the third from 4·5 to 13·5, etc., we get a 'three times' geometric classification* into

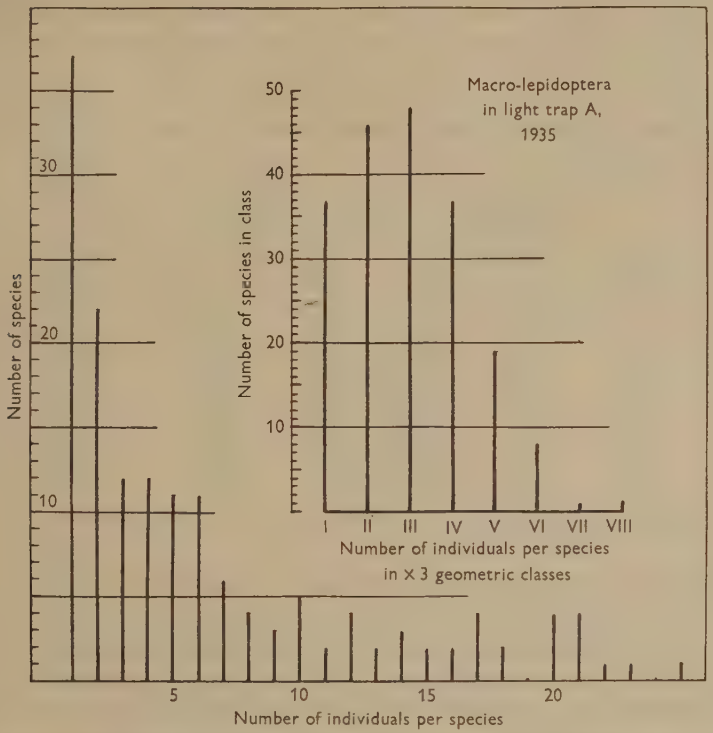

Fig. 1. No. of species of Macro-lepidoptera with different numbers of individuals captured in a light trap (A) at Rothamsted in the year 1935. First with the numbers of individuals per species on an arithmetic scale, and second in × 3 geometric classes as explained in the text. Data in Table 1.

which the original integer observations fit very simply and require no splitting. The integers in the classes are thus

Class			Class	
I	1		VI	122–364
II	2–4	inclusive	VII	365–1,093
III	5–13	,,	VIII	1,094–3,280
IV	14–40	,,	IX	3,281–9,841
V	41–121	,,	X	9,842–29,524

To give an example, the number of species of moths represented by 1, 2, 3, 4, etc., individuals trapped in a light trap at Rothamsted during the year 1935 is shown in Table 1 and in Fig. 1, at first on an arithmetic integer scale and then on a × 3 geometric classification.

* If for the material in hand this grouping is too close, a × 5 classification can be made with the dividing lines at 0·5, 2·5, 12·5, 62·5, etc., i.e. with the integers 1–2, 3–12, 13–62, etc. Or any larger *odd* number can be used for multiplication.

It will be seen that on an arithmetic scale these data give a 'hollow curve' somewhat resembling a hyperbola, but when arranged in $\times 3$ classes there is a curve resembling a truncate normal distribution with the peak between classes II and III.

If calculations are made for different sized samples taken from a population arranged in a logarithmic series the number of species in the $\times 3$ classes are as shown in Table 2 and in Fig. 2. The distributions are similar for all samples with the same average number of individuals per species—that is to say also with the same value of x.

Table 2. *Theoretical frequency distribution of species, in $\times 3$ classes, in samples of different sizes taken from a population arranged in a logarithmic series with $\alpha = 100$**

Size of sample				Number of species in class			
Individuals	Species	Average individuals per species	x	I (1)	II (2–4)	III (5–13)	IV (14–40)
43	37	1·16	0·3	**30**	5·60	0·065	—
100	69	1·44	0·5	**50**	18·23	1·09	—
233	120	1·94	0·7	**70**	41·94	8·32	—
900	230	3·91	0·9	**90**	81·28	47·91	10·94
1,900	300	6·34	0·95	**95**	94·07	72·61	33·50
2,173	306	6·95	0·956	**95·6**	**95·6**	—	—
3,746	360	10·5	0·974	97·4	**99·77**	88·56	58·65
9,900	461	21·47	0·990	99·0	**105·36**	101·00	86·05
19,900	531	37·48	0·995	99·5	**106·95**	105·27	97·25
99,900	691	144·6	0·999	99·9	108·04	**108·50**	107·18
Inf.†	Inf.	Inf.	1·000	100	108·33	109·68	109·84

* For other values of α the numbers in the above table must be multiplied by $\alpha/100$.
† Hyperbolic or harmonic series.

It will be seen that for small samples the curve is of the 'hollow' type even on this geometric classification. When, however, we reach a sample with $x = 0{\cdot}956$ (or just under seven individuals per species on an average in the sample), the number of species in class II becomes equal to class I. With just over 100 individuals per species class III becomes greater than class II. Any samples larger than this give a curve with a peak which gradually moves further along the class ordinate. When the sample is infinite x becomes 1 and the log-series becomes a hyperbolic or harmonic series. In this case the frequency distribution is 100 species (i.e. α) in class I, rising to 108·3 in class II and then becoming constant just below 110 in all further classes. Thus one of the characteristics of the log-series is that the number of species in the peak class cannot (except by accidental error) be more than 10% above the number of species with one individual however large the sample.

We thus have in animal populations three different ways of distinguishing between the frequency distribution of species and individuals based on the logarithmic series and on the log-normal:

(1) From changes in the number of species with one individual (n_1) in samples of increasing size from the same population.

(2) From the rate of increase of number of species in relation to sample size with very large samples.

(3) From the distribution of species in $\times 3$ (or any other geometric) grouping of classes of abundance.

All these three methods are most useful with large samples, as the resemblance between the two theories is so close in small samples as to make them practically indistinguishable. The third method has the advantage of requiring only a single large sample.

It is next necessary to examine the data available to see how this can be analysed to show any of the above differences.

The most complete series of samples from an animal population that are available are those taken from wild mixed insect populations by means of light traps.

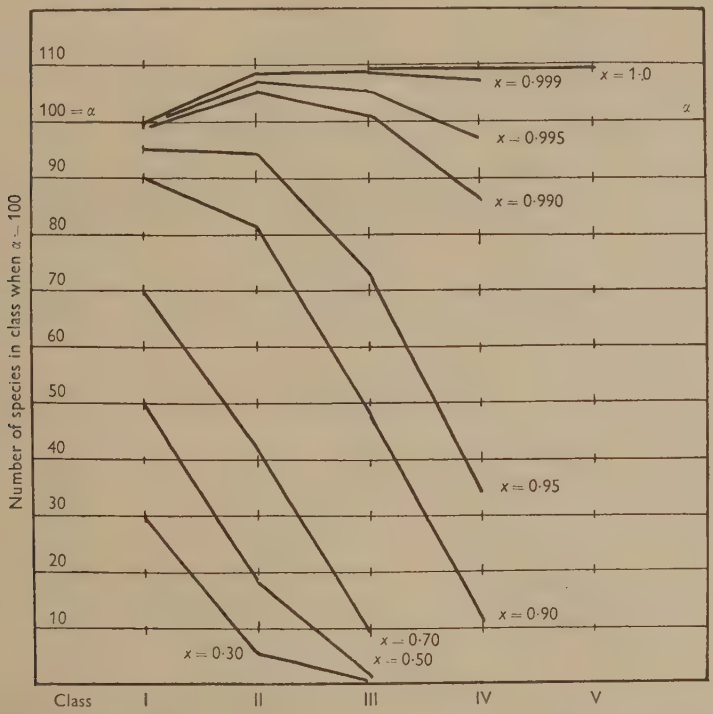

Fig. 2. The theoretical relation between the sizes of × 3 class groupings of species with different numbers of individuals, in samples of increasing size (and hence increasing values of x) taken from a population arranged in a logarithmic series with the index of diversity = 100. Data in Table 2.

In the course of 8 years trapping by this method at Rothamsted Experimental Station, Harpenden (about 25 miles north of London) nearly 100,000 Macro-lepidoptera were captured and identified. A total of nearly 350 species were represented from the families Noctuidae (Agrotidae), Geometridae, Sphingidae, Bombycidae, Arctiidae, Lithosiidae and a few other related families. Of this total nearly 33,000, representing 285 species, were taken in a single trap (A) which was in continuous use in one place for two complete periods of 4 years (Williams 1939, for first 4 years).

A summary of the data from this trap is shown in Table 3 and in Fig. 3. The table gives the number of individuals and of species, and the distribution of species in

Table 3. *Frequency distribution (in × 3 classes) of Macro-lepidoptera caught in a single light trap (trap A) at Rothamsted Experimental Station during 1933–37 and 1946–50*

Period	Individuals	Species	Average individuals per species	Number of species with different numbers of individuals (geometric classes × 3)								
				I (1)	II (2–4)	III (5–13)	IV (14–40)	V (41–121)	VI (122–364)	VII (365–1093)	VIII (1094–3280)	IX (3281–9841)
				One-eighth of year (Av.)								
1933	440	89·6	4·9	**36·0**	27·3	19·3	7·0	0·1	—	—	—	—
1934	409	86·8	4·7	**34·3**	27·8	16·4	8·3	0·3	—	—	—	—
1935	855	107·1	8·0	**39·5**	34·4	21·1	9·0	2·0	0·9	0·3	—	—
1936	250	67·6	3·7	**33·6**	19·4	10·9	3·6	0·1	—	—	—	—
	Average of 4 years			**35·8**	27·2	16·8	7·0	0·6	0·2	0·1	—	—
				Whole year								
1933	3,454	173	20·0	32	**54**	36	28	18	5	—	—	—
1934	3,276	168	19·5	33	**42**	39	35	12	7	—	—	—
1935	6,530	191	34·2	37	**47**	45	36	18	6	1	1	—
1936	1,961	154	12·7	**54**	34	35	21	8	2	—	—	—
	Average of 4 years			39·0	**44·3**	38·8	30·0	14·0	5·0	0·3	0·3	—
1946	3,124	156	20·0	39	**43**	40	17	14	1	2	—	—
1947	3,786	184	20·6	45	**53**	36	28	17	4	1	—	—
1948	3,771	187	20·2	47	**54**	43	22	18	1	2	—	—
1949	6,107	191	32·0	48	**49**	**49**	23	16	3	2	1	—
	Average of 4 years			44·7	**49·8**	42·0	22·5	16·3	2·3	1·8	0·3	—
	Average of 8 years			41·9	**47·0**	40·4	26·3	15·2	3·6	1·0	0·3	—
				Series of years								
1933–36 (4 years)	15,221	234	65·0	34	41	**47**	46	34	24	7	1	—
1946–49 (4 years)	16,972	254	66·8	45	43	**57**	52	29	21	5	1	1
	Average of two periods			39·5	42	**52**	49	31·5	22·5	6	1	0·5
All 8 years	32,853	285	115·3	38	41	48	**67**	43	28	14	5	1

geometric $\times 3$ classes for periods varying from $\frac{1}{8}$ of a year (i.e. every 8th day throughout the year) to the total catch for 8 years.

It will be seen that the peak number of species is in class I for the $\frac{1}{8}$ year (average number of individuals per species 4–8); and the peak is in class II for whole years

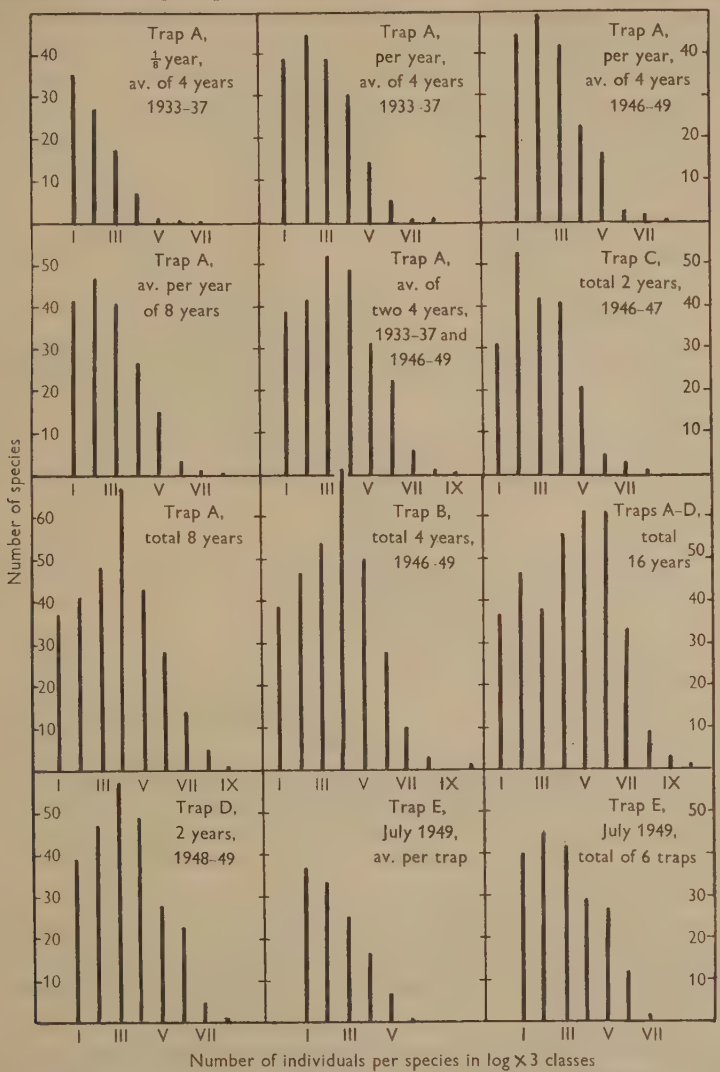
Trap A, ⅛ year, av. of 4 years 1933–37
Trap A, per year, av. of 4 years 1933–37
Trap A, per year, av. of 4 years 1946–49
Trap A, av. per year of 8 years
Trap A, av. of two 4 years, 1933–37 and 1946–49
Trap C, total 2 years, 1946–47
Trap A, total 8 years
Trap B, total 4 years, 1946–49
Traps A–D, total 16 years
Trap D, 2 years, 1948–49
Trap E, July 1949, av. per trap
Trap E, July 1949, total of 6 traps
Number of species
Number of individuals per species in log × 3 classes

Fig. 3. Relation between number of species and numbers of individuals (the latter in $\times 3$ geometric classes) in catches of Macro-lepidoptera in light traps at Rothamsted. Original data in Tables 3 and 4.

(average individuals per species 19–34) except for the year 1936 when the peak was in class I and the average number of individuals per species only 12·7.

In the two 4-year periods, with an average number of individuals per species of 65–67, the peak is in class III and in the total of all 8 years, with an average of 115

individuals per species, the peak is in class IV. Although there is not very much difference between these results and the relation between peak, class and average individuals per species as shown in Table 2 for the logarithmic series, there is a slight tendency for the peak to be in a higher class than that expected. The height of the peak is, however, in the larger samples (4–8 years) distinctly more than 10% above class I, thus departing from this characteristic of the log-series. A study of the changes in numbers in class I on the contrary shows a slight rise (36–42) from the average for

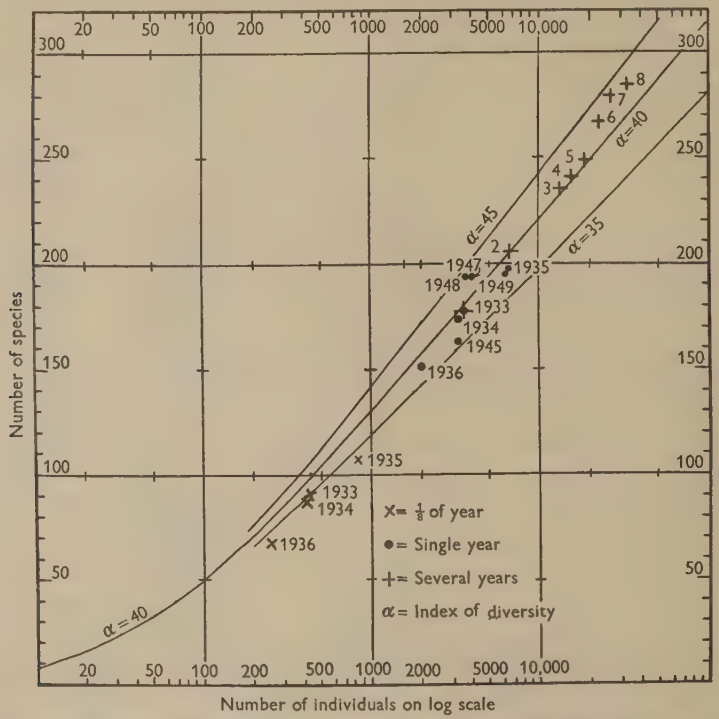

Fig. 4. The relation between increasing size of samples and increasing number of species in catches of Macro-lepidoptera in a light trap (A) at Rothamsted in periods varying from ⅛ year to 8 years during 1933–36 and 1946–49.

⅛ year to the average for 1 year, but only a slight indication of a fall after this to 39·5 for 4 years and 38 for 8 years. The increase in number of species with increased sample size is shown graphically in Fig. 4, and it will be seen that so far from falling below the number expected by the log-series in higher values, there is actually an excess. In other words, the diversity of the sample on the basis of the log-series is increasing.

There is, however, a disturbing factor from the pure theory in the way the samples have been taken. The larger samples have been taken over a longer period than the smaller (except in the case of the ⅛-year samples) and are thus not strictly comparable. There is no doubt that this accounts for the steady increase in diversity, as the population sampled during 8 years by one trap will not give the same result as a trap catching eight times as many insects in one year. This increase in diversity will also

affect the changing values of n_1 (or class I) as already discussed above; a slightly higher class I would be expected in the larger samples, and so the small fall which has been found is more significant than it would otherwise be.

In Fig. 5 the numbers of species in the different $\times 3$ classes in trap A for different size samples have been shown one on top of the other with the position of class I changed (logarithmically) to allow for the increased size of samples as shown on a horizontal scale below the diagram. For example, if the sample size were increased three times, the position of class I would move one class interval to the left. It will be

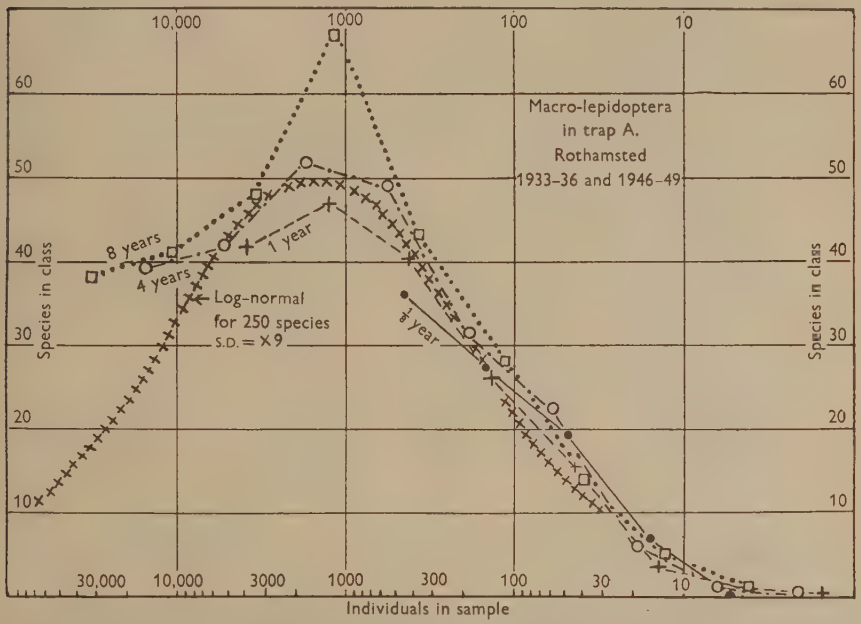

Fig. 5. Frequency distribution of species with different numbers of individuals (in $\times 3$ geometric classes) of Macro-lepidoptera caught in a light trap (A) at Rothamsted in different periods from $\frac{1}{2}$ year to 8 years. The resulting distributions arranged so that the position of class I varies according to the size of the sample on a horizontal scale reading from right to left. The superimposing of the curves illustrates Preston's theory of sampling from a log-normal distribution.

seen that the whole pattern tends to form a continuous curve, resembling Preston's suggestion that with a log-normal population samples of different sizes are truncate log-normals represented by moving the zero line on the original population curve. Grundy's work shows that this is approximately correct except for very small samples.

Superimposed on these curves is a log-normal calculated to fit 250 species with a standard deviation equal to two $\times 3$ groups (i.e. $\times 9$). It will be seen how closely the observed results fit to this log-normal distribution, with the exception of the total of 8 years. It is questionable whether in this case the two periods of 4 years, separated by force of circumstance by a gap of 9 years, should really be combined into a single sample. The figure is not meant to demonstrate mathematical identity, but to show a trend in observed biological data which is approximately paralleled in the theory of sampling from a log-normal population.

Table 4. *Frequency distribution of abundance of Macro-lepidoptera in various light traps at Rothamsted Experimental Station*

Period	Individuals	Species	Average individuals per species	Number of species with different numbers of individuals. Geometric classes (×3) I (1)	II (2–4)	III (5–13)	IV (14–40)	V (41–121)	VI (122–364)	VII (365–1093)	VIII (1094–3280)	IX (3281–9841)	X (9842–29,542)
Trap B													
4 years 1946–49	35,428	304	116·5	39	47	54	**72**	50	28	10	3	0	1
Trap C													
2 years 1946–47	5,972	197	30·3	31	**53**	42	41	21	5	3	1	—	—
Trap D													
2 years 1948–49	12,456	249	50·0	39	47	**57**	49	28	23	5	1	—	—
All four traps all years													
16 Trap years	87,400	346	252·6	37	47	38	56	**61**	**61**	33	9	3	1
Traps E 1–6. Month of July 1949 only, in woodland													
Average per trap	1,230	119·7	10·3	**36·8**	33·7	25·8	16·2	7·0	0·2	—	—	—	—
Total of six traps	7,378	197	37·5	40	**45**	42	29	27	12	2	—	—	—
Trap R (mercury vapour), August 1950													
11 days in garden	3,349	106	31·6	24	**31**	24	14	7	2	3	—	—	—
15 days in woodland	5,232	84	62·3	**24**	19	**23**	11	5	1	—	—	1	—

To overcome the difficulty of comparing samples taken over different periods a trapping experiment was made during the month of July 1949, in which six traps were working simultaneously in a small woodland at Harpenden (traps E 1–6). The results showing the average per trap and the total of all six traps are shown in Table 4 and Fig. 3. The average number of individuals per species was 10·3 in the single trap, and the peak in class I, while in all six traps together the peak was in class II with an average of 37·5 individuals per species. The log-series (see Table 2) would require a peak between classes I and II in the first case and between II and III in the second, so that these figures do not clash with the observed. The total of all six traps is still too small to provide a strict criterion.

During the period 1946–50 several other traps (B, C and D) were run in different localities in the same neighbourhood as shown in Table 4 and Fig. 3. Trap B over 4 years caught 35,000 moths with an average of 116·5 individuals per species and a peak in class IV (above that expected by the log-series).

Table 5. *Macro-lepidoptera caught in mercury-vapour light trap (G) at Rothamsted during the nine months March to November 1951*

Class	Individuals per species	Noctuidae	Geometridae	Other families	Total
I	1	14	12	5	31
II	2–4	18	13	**14**	45
III	5–12	25	21	9	55
IV	13–40	30	**22**	**13**	**65**
V	41–121	**32**	5	6	43
VI	122–364	12	1	4	17
VII	365–1,093	4	—	—	4
VIII	1,094–3,280	4	—	—	4
IX	3,281–9,841	1	—	—	1
Total species		140	74	57	265
Total individuals		23,425	1,258	1,617	26,300
Average individuals per species		167·3	17·0	13·7	99·3

The total of all four traps in a total of sixteen trap-years caught 87,000 moths with an average of 253 individuals per species and a peak between classes V and VI. Too much emphasis must not, however, be laid on this grand total owing to the long period of time and the widely different conditions under which the figures were obtained.

Both in trap B (4 years) and in the total of all traps the increase of the peak above the value of class I is far beyond the limit of 10% required by the log-series. The rise is from 39 to 72 in trap B and from 37 to 61 in all four traps.

In order to get a still larger sample in a shorter time two mercury vapour ultraviolet light traps were started in March 1951 (after very short trials in 1950) and were run continuously during 1951 under the supervision of Mr M. Hosni; one (F) inside the woodland already referred to and one (G) just outside in a locality where no trapping had previously been done. At the end of 9 months (March to November) in the trap outside the wood 26,300 Macro-lepidoptera had been captured belonging to 265 species. This is a much greater number than had ever before been captured in so short a time, and is indeed 60% more individuals and 25 more species than were caught in the whole of the first 4 years trapping with trap A. The results on a $\times 3$ geometric classification are shown in Table 5 and Fig. 6.

These results support again the idea that large samples depart from the logarithmic series in the direction of the log-normal, as in each family subdivision, and in the total, the peak class has a value about double that of class I, but even with this large catch the distribution is not symmetrical about the peak.

Apart from light-trap catches, very large samples of insect populations which are randomized for abundance, and in which all or very nearly all of the species have been identified, are not often recorded; but some examples are given by Palmèn (1944) of great masses of Coleoptera washed in from the sea and piled up in long rows on the southern shores of Finland. They cannot be strictly said to have been taken from one particular association, and we do not know for certain if they have been washed out to sea by flooded rivers or have been brought down on the surface of the ocean by heavy rains or some similar cause. Over 970 species of beetles were identified by Palmèn in nine such aggregations. For each species in a large random sample from each of the aggregations he gives the actual number of individuals if it is below 50;

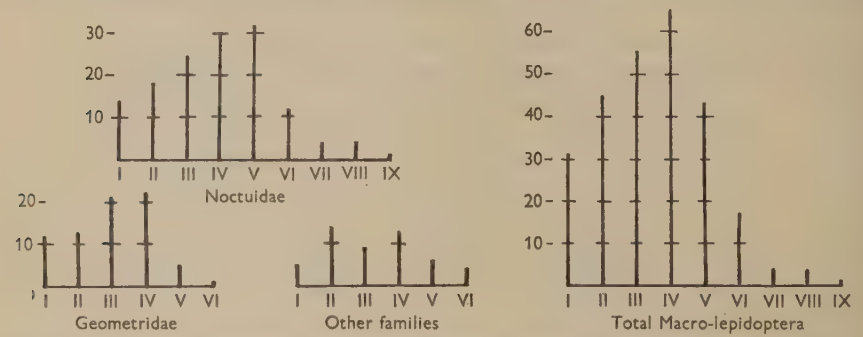

Fig. 6. Distribution of numbers of species with different numbers of individuals (the latter in $\times 3$ geometric classes) as shown by captures of Macro-lepidoptera in a light trap (G) at Rothamsted from March to November 1951. Based on 26,300 individuals belonging to 265 species. Data in Table 5.

higher numbers are grouped into over 50, over 100, over 200, over 300, over 500, over 1000, and 'infinite'. It is thus not possible to get the total number of individuals in a sample or the average number of individuals per species, as by far the greater proportion of individuals in any population is made up from the few most abundant species. The structure of two samples, with the actual number of species with up to 50 individuals, is given in Table 6 and Fig. 7.

The first sample (Palmèn's Pa 1) was taken on 12–13 June 1939, and contained 393 different species. It will be seen that in this sample there is not a true 'hollow curve' as the number of species with two individuals is greater than the number with one. This is the only random sample of insects that I have so far traced in which this condition is found. The frequency distribution on a $\times$ 3 scale shows a peak in class II (2–4 individuals), and might easily be a portion of a log-normal distribution. Class II is more than 100% above class I and so the distribution is definitely not of the logarithmic series type.

The second sample (Palmèn's Pa 3) was taken from an aggregation on 4–5 July 1939, and contained 466 species. In this the number of species represented by one individual is larger than that by 2, but not as different as is required by the logarithmic

series, in which the number with 2 must always be less than half the number with one. The classification into $\times 3$ logarithmic classes gives a maximum in class II, as before, with class II over 60% above class I, and a close resemblance to a log-normal distribution.

Table 6. *Numbers of species of Coleoptera with different numbers of individuals found by Palmén (1944) in drifts along the sea-shore in Finland*

(The figures in parentheses are sub-totals for the geometric $\times 3$ classes.)

SAMPLE I

Individuals per species	Species	Individuals per species	Species	Individuals per species	Species
1	72 (72)	13	5 (90)	28	1
2	91	14	4	29	1
3	47	15	0	39	1 (29)
4	23 (161)	16	6	50	2
5	30	17	1	>50	14
6	19	18	3	>100	5
7	8	19	3	>200	2
8	12	20	3	>300	1
9	3	21	2	>500	8
10	2	22	1	'∞'	9
11	4	25	1	Total species	393
12	7	26	2		

SAMPLE II

1	111 (111)	15	5	32	1
2	87	16	4	33	1
3	59	17	5	34	1
4	35 (181)	18	1	36	2 (37)
5	29	19	1	49	1
6	20	20	0	50	1
7	6	21	2	>50	11
8	10	22	1	>100	9
9	17	23	1	>200	4
10	3	24	1	>500	1
11	3	25	1	>1000	1
12	7	29	2	'∞'	10
13	4 (99)	30	1	Total species	466
14	5	31	2		

Since the general principles of the structure of populations are not likely to be confined to any one group of animals, it is interesting to see to what extent the results of surveys and censuses made by ornithologists will support or extend those based on

Table 7. *Data for bird populations, (1) from Stewart & Aldrich (1949), (2) from Saunders (1936)*

	Total species	Total pairs	× 3 class I	II	III	IV	V	VI	VII	VIII
(1) Appalachian Mountains	24	100	**10**	6	6	2	—	—	—	—
(2) Quaker Run Valley	79	14,348	2	9	12	**15**	**14**	**16**	8	3

insect populations. Table 7 shows two sets of data on bird population from the United States; in each case the original numbers have been reclassified on a $\times 3$ basis. The figures in both these cases are of breeding pairs. The average number of pairs per species is 4·2 in the first with a peak in class I, and 180 in the second with a rather flat

peak ranging from classes IV to VI. The small Appalachian sample is close to a logarithmic series, as one calculated to fit 100 pairs in 24 species would give the first term 9 and the second 4·05 as compared with observed values 10 and 4. The position

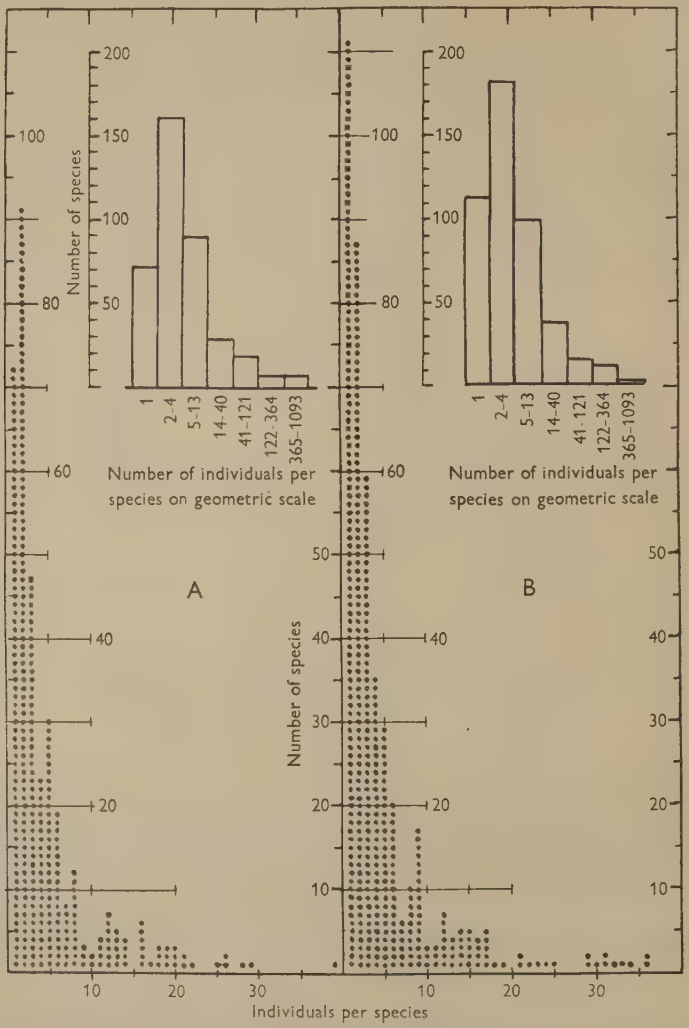

Fig. 7. Distribution of numbers of species of Coleoptera with different numbers of individuals in two samples taken by Palmèn from great drifts of insects found on the sea shore in Finland in 1939. The number of individuals is shown both on an arithmetic scale (up to 40) and on a geometric ×3 scale (up to 1093 individuals per species). Data in Table 6.

of the peak for the log-series has not been calculated for such high average numbers of units per group as that found in the second sample, but the height of the peak is eight times as large as class I, which is impossible for the log-series, but quite possible for a log-normal distribution.

To get a still greater 'sample' I asked Dr James Fisher if he could group all the known nesting land-birds in England and Wales in categories of abundance in powers of 10, i.e. whether the average number of individuals present in a breeding season

Table 8. *Estimate by Dr James Fisher of number of species of nesting land-birds in England and Wales with different levels of abundance*

Class	Number of individuals per species	Number of species
I	1–10	7
II	10–100	9
III	100–1000	22
IV	1000–10,000	42
V	10,000–100,000	32
VI	100,100–1 million	16
VII	1–10 million	12
VIII	over 10 million	2*
	Total	143

* Just above 10 million.

was 1–10, 10–100, 100–1000, etc. He has done this for me and the details have been published (Fisher 1952). A summary of the number of species in each group is given in Table 8.

The results, shown graphically in Fig. 8, give a very close approximation to a log-normal distribution with a mean near the top of class IV at about 8000 individuals per species, and a standard deviation of $10^{1.4}$. It bears no resemblance to a logarithmic

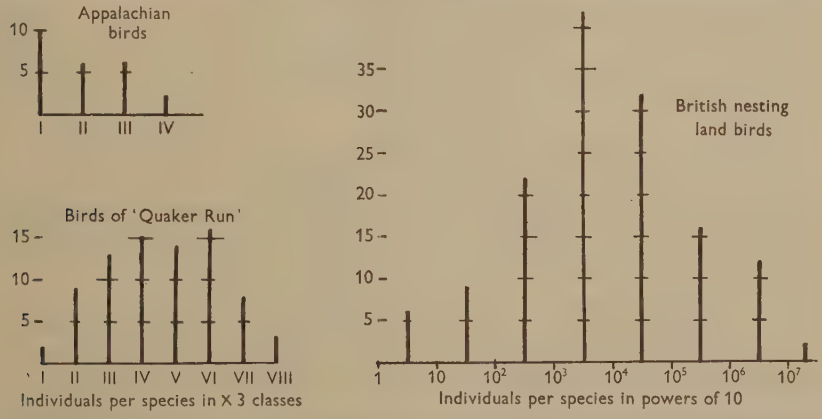

Fig. 8. Distribution of numbers of species of birds with different numbers of individuals in two samples of American birds (with the number of individuals on a × 3 geometric scale), and in an estimate of the total population of 144 nesting landbirds in England and birds in England and Wales, with the numbers of individuals on a × 10 geometric scale. For data see Tables 7 and 8.

series. The total number of birds included in the census is about 63 million, giving an arithmetic mean of about 440,000 individuals per species, with a peak on the × 3 classification near the top of class IX (3281–9840). Fig. 9 shows the same data on 'probability' paper showing the very close relation of the observed figures to the straight line required by the log-normal distribution, with a mean at 8000, and a standard deviation of $10^{1.4}$.

SUMMARY AND DISCUSSION

Thus we see that a survey of large samples taken from mixed animal populations tends to support the idea that the distribution of species with different numbers of individuals is nearer to the log-normal than to the log-series form. This suggestion was first made by Preston (1948), and has also been independently suggested to me by Mr W. S. Volkers, a student of statistical biology at the University of Utrecht in Holland.

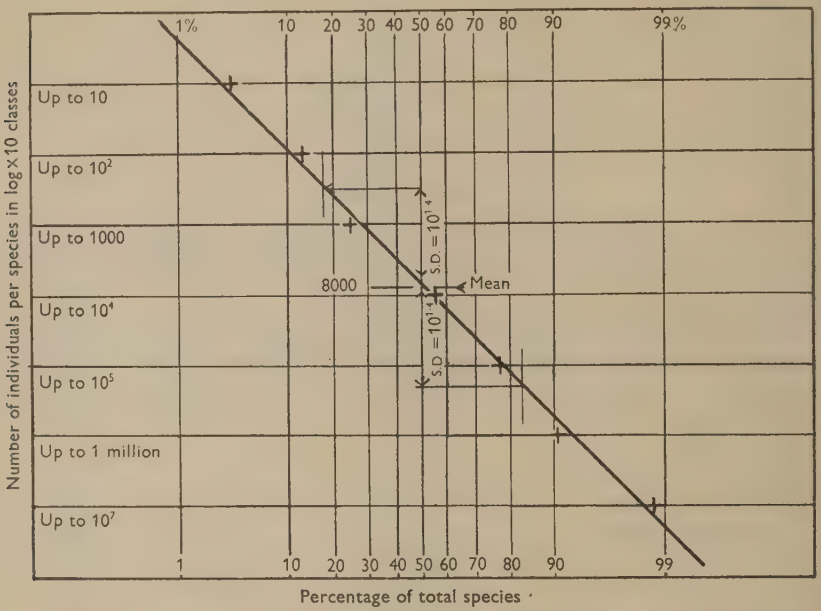

Fig. 9. James Fisher's data (Table 8) on the relative abundance of British nesting land-birds plotted on log-probability paper, so as to show the relation between the accumulated percentage total of species up to each level of abundance. The recorded points are very close to the straight line which shows a mean at $10^{3\cdot9}$ (=approx. 8000) individuals per species, and standard deviation of $10^{\pm1\cdot4}$.

The mathematical problems relating to the question of sampling from a log-normal population, and of fitting a log-normal distribution to data, have been recently taken up by Mr P. Grundy of the Statistical Department at Rothamsted. The problem is made more complex by the fact that most biological data are incomplete, as it is not possible to say how many species present in the population were not represented in the sample. His work is in the process of publication (Grundy 1951).

The main differences in conception, apart from the increased mathematical complexity, between the log-series and the log-normal are:

1. The former postulates no limit to the numbers either of species or of individuals in the population from which the samples are taken, while the log-normal implies a finite number of species, although the number of individuals is theoretically unlimited.

2. Three parameters are necessary to define a log-normal, whereas two are sufficient for a log-series. As a result to the total number of individuals and of species in the

sample, which is sufficient to define a log-series, must be added a third constant fixing in some way the standard deviation of the curve, before a log-normal can be fitted to given data.

3. With increasing size of sample from a log-series population, the relation between the number of species and the log-number of individuals tends to a straight line (Fig. 4), but with a log-normal population the curve is sigmoid and flattens out as it approaches the limit of the total number of species in the population which is being sampled.

4. There is with the log-normal a decline in the number of species with one individual (n_1, or class I) after the sample is large enough to include about 50% of the species in the population, which does not occur if the distribution is of the log-series form.

5. There is in the log-normal distributed population the gradually increasing difference between the number of species with one individual (n_1 or class I), and the number in the peak class as sample size increases. This difference is limited to 10% in a log-series population.

It is evident that many more examples of large random samples of animal populations, with accurate counts and determination of species, are required before the general form or forms of distribution of the species, and hence the pattern or balance of the populations, can be determined.

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THE EXTERMINATION OF ANIMAL POPULATIONS BY ARTIFICIAL PREDATION AND THE ESTIMATION OF POPULATIONS

By J. P. GLASGOW

East African Tsetse and Trypanosomiasis Research and Reclamation Organization

(With 1 Figure in the Text)

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INTRODUCTION

This paper falls into two parts, as the title indicates. They are linked together by the circumstance that both are referred to the same body of data (Table 1).

The term 'Artificial Predation' is here adopted to include all cases where a population of animals is directly attacked by man, by shooting, trapping, hand collection or other similar methods. The term implies that man is the predator. Cases in which man affects an animal population indirectly by altering the animals' environment, for example destruction of a forest leading to the extermination of monkeys, are not artificial predation. Cases in which poison is spread in an essential part of the animals' environment as in mosquito control by insecticides, are also not artificial predation. Nevertheless ideas parallel to those developed in this paper have been usefully applied to a case in which a population of blood-sucking flies (Tsetse) was attacked by introducing into their environment a number of cattle externally treated with an insecticidal preparation (Whiteside 1949). The distinction is sometimes fine, but it is proposed to define the term as including cases in which the animal finds and eats a poison, but excluding cases where the poison is made to seek the animal (mosquito control, gas warfare, fumigation). The justification for this distinction is that most animals are available to a predator only when they are themselves seeking for food.

It is not generally agreed whether artificial predation is or is not a feasible method of exterminating a population of animals. On the one hand, artificial predation nearly exterminated the American bison (Peattie 1943; Calahane 1944), and is said to have completely exterminated the passenger pigeon (Abbot 1944). It exterminated the quagga (Lydekker 1926, p. 41). It exterminated the tsetse-fly, *Glossina palpalis*, on the island of Principe (Austen & Hegh 1922), but failed to exterminate the same fly on the island of Mugasiro (Koch 1914), although it did exterminate this fly in an isolated patch of bush on a small river (Glasgow & Duffy 1947). It has been suggested (Oakley

1950) that the success of the Gravettians as hunters may well have contributed to the extermination of mammoths. It is agreed (see, for example, Hamilton 1948, and Mackintosh 1948) that it is essential to regulate the whaling industry, in order to prevent the extermination of these animals, or at least their reduction to a level so low that the industry could no longer exist. For the elimination of warble-flies (Oestridae) collection of larvae has been recommended in Bavaria (Zaubzer 1932) and of adults in Uzbekistan (Sapogov 1947); and the collection of larvae successfully eliminated two species (*Hypoderma bovis* De G. and *H. lineatum* De Vil.) from Clare Island, Ireland, between 1915 and 1920 (Lyle 1947). According to Ford (1945, p. 142) it is probable that 'over-collecting' has exterminated certain local colonies of rare species of butterflies in Great Britain.

On the other hand, one of the biggest attempts to control an insect pest by artificial predation has been the Mauritius work against *Clemora* (*phytalus*) *smithi* Arrow. The work was carried out on a basis approaching a 'Second industry', 4000 millions of beetles being destroyed in the course of 26 years. Since the cessation of hand collection the infestation has become no worse (Moutia & Mamet 1946). The hand picking of *Antestia* from coffee trees in Kenya was studied by Le Pelley (1935) who concluded that the cost of picking an adequate percentage was almost invariably prohibitive. Certain theoretical aspects of Le Pelley's work will be discussed later.

THEORETICAL CONSIDERATIONS

It is obvious that the habits of the animals subject to predation are all-important. Consider first a population of completely immobile animals, such as a bed of oysters exposed at low tide. Suppose that during one low tide we have time to pick one-quarter of all the oysters. Clearly if we keep at it for 4 days we shall have picked them all, and extermination will be complete in 4 days. Consider now a population of mobile animals, such as trout in a stream exposed to predation by anglers. Suppose that during one day the anglers remove one-quarter of the trout in the stream. The second day they will remove one-quarter of the remainder and so on. If the initial population was P, the catches on successive days will be

$$\tfrac{1}{4}(P),\ \tfrac{1}{4}(\tfrac{3}{4}P),\ \tfrac{1}{4}(\tfrac{9}{16}P),\ \ldots,\ \text{etc.}$$

This is a geometrical progression in which the first term is $\frac{1}{4}P$ and the common ratio is 0·75. The sum of an infinite number of terms of the progression is

$$\tfrac{1}{4}P/(1-0{\cdot}75)=P.$$

Thus at first glance the anglers have to continue for an infinite number of days in order to catch all the trout. In practice this not so. If we have reason to believe that P is less than a hundred, we may well be content to catch 99% of the population.

The sum of n terms of a geometric progression is given by the formula

$$S_n=a(1-r^n)/(1-r),$$

where r is the common ratio, and if $S_n=0{\cdot}99$, then

$$n=-2/\log(1-r),$$

where f is the fraction of the population caught on any one day (i.e. $\frac{1}{4}$ in the trout

example). From this formula we calculate n, the number of days it would take to remove 99% of the population for various values of f:

f	0·75	0·5	0·4	0·3	0·25	0·2	0·1	0·01
n	3	7	9	13	16	21	43	454

From a purely mathematical standpoint $f=0{\cdot}5$ is more than twice as effective as $f=0{\cdot}25$, and $f=0{\cdot}1$ is more than ten times as effective as $f=0{\cdot}01$. The formula for the 99·99% point is

$$n=-4/\log(1-f),$$

i.e. in time 99% is half-way to 99·99%. If we had a vessel of salt water containing P molecules of salt, and we drank each day a certain fraction f of the water, afterwards filling the vessel up with distilled water and stirring, then the population of P molecules would diminish exactly according to the rules given above. We must now consider the ways in which animals differ from molecules.

It was noted above that oysters would be easier to exterminate than trout. There are also intermediate conditions such as that of zebras and locusts, which occur in motile swarms. The existence of such swarms is of assistance to the artificial predator. Other animals are what is known as over-dispersed, i.e. they appear to avoid other members of the same species, either because they have a territorial system or for some other reason. This habit also might assist the artificial predator as he would know not to waste time looking for another prey in a place where he had already found one. An animal randomly dispersed would appear to be the most difficult to find.

By 'control factor' is meant something which acts on a population when it is dense, preventing or tending to prevent its further increase, but which has a progressively smaller effect on a diminishing population. The term was used by Nicholson (1933), who gave as examples competition for food, competition to avoid being eaten, and competition for a limited number of suitable locations. Up to this point I have tacitly assumed that animal populations are constant until disturbed—that they are in what Nicholson calls the 'steady state'. This, of course, is not true of natural populations, which normally fluctuate with a seasonal, or longer, periodicity, but provided these fluctuations are moderate they will not upset the reasoning which has been used so far. However, Nicholson shows that when an insect population is controlled by a specific entomophagous parasite, population fluctuations are produced by the reactions of the two species, even in a constant environment, and these fluctuations increase as time goes on. In nature, the end result of this situation is that the population of animals is split up into a number of small groups, the positions of which constantly change. The population density taken over the whole area concerned is then much smaller than it would be if it were possible to maintain the theoretical 'steady density'. The introduction of artificial predation into such a system may damp these violent fluctuations and so cause the population to be maintained at a higher density than it otherwise would be. Le Pelley (1935) gives what appears to be an example of this, where *Antestia* was hand-picked from a coffee plantation continuously for 15 months. During this time the *Antestia* population remained at a steady high density, which is stated to be quite unusual.

It is not often that we know enough about an animal population to be able to calculate in advance what effect control factors would have upon an attempted artificial

predation. But it is possible and useful to consider the maximum possible effect which such factors could have. Thus a tropical beetle might lay 100 eggs per female, and have four generations a year. In the steady state only two of these eggs need to give rise to breeding adults. Assuming that control factors destroy the other 98, and that they will cease to operate at low densities, we see that this beetle could double its population in a day. Artificial predation could not be relied upon to exterminate this beetle unless it were possible to destroy the whole population in one day. Consider, on the other hand, a herbivorous mammal which drops 10 calves in the course of 10 years. There are only 8 spare calves in 10 years, or 0·8 in one year. From a herd of 1000 cows and 1000 bulls there would be 800 spare animals a year, but shooting three a day would be enough to ensure extermination (because $3 \times 365 > 800$). This line of reasoning seems to be a sufficient explanation of why artificial predation has exterminated certain populations of mammals and of very slow-breeding insects, whereas it has been quite useless against faster-breeding insects.

In practice it is difficult to arrange an artificial predation which is independent of the density of the population. The angler in our trout example would lose interest in the stream as trout became rare, and doubtless when *Hypoderma* becomes rare farmers tend to forget to squeeze the larvae out of the backs of their cattle. There is also a selective effect which may be important, since the animals which are least wary will be likely to be caught first. Also if there is competition for food, as the population diminishes the food becomes relatively abundant, and the animal is less liable to predation because it has to spend less time searching for food. This is equally true whether we think of a trout caught on a bait, or a rabbit being shot while grazing. Special measures are therefore likely to be necessary to ensure that f, the fraction of the population removed in unit time, does not seriously diminish. If at any time during the course of an extermination the prey population becomes static, it will mean either that the initial value of f was small, and is now being absorbed by the natural power of increase of the species, which was previously destroyed by control factors whose action has diminished as the population diminished, or that the value of f, possibly high enough in the beginning, has fallen too low, for one of the reasons already mentioned. In either case no further progress can be made without raising the value of f by increasing the intensity of the artificial predation.

PREVIOUS STUDIES OF ARTIFICIAL PREDATION

Le Pelley (1935), picking *Antestia* off coffee trees, showed that the total percentage of the population picked at any stage was given by the formula

$$P = 100\,(1 - (0{\cdot}89\,e)^{-t}),$$

where P represents the percentage hand-picked of the total *Antestia* present, and t is the time in hours spent picking (but picking went on for only 15 minutes each day). This formula is only another way of saying that the catches followed a geometrical progression in which r, the common ratio, $= 0{\cdot}8019$, and the fraction of the population caught per day (of 15 minutes work) $f = 0{\cdot}1981$. The experiment continued for only 8 days, by which time 83% of the population had been caught. During this time, however, since the catches followed the expectation extraordinarily closely, none of the possible complications discussed above can have come in to play.

Leslie & Davis (1939) trapped rats (*Rattus rattus*) for 6 weeks in Freetown. The total catches per week followed very close to a geometrical progression with $r = 0{\cdot}7969$, $f = 0{\cdot}2031$.

Emlen, Stokes & Davis (1949) trapped rats (*R. norvegicus*) in Baltimore, Maryland. They state that, during intensive trapping of a city block, 'the daily catch...typically declined in a geometric curve'. Their figure 1 graphs the catches for 12 days in a typical, heavily infested city block. The agreement with a geometrical progression is not nearly so close as it was in the two cases considered above, but there is no trend which might lead one to suppose there was a real departure from the geometrical theory.

Table 1. *Weekly catches of* Glossina palpalis *in Block VII, Kuja River, beginning 15 July 1946*

	Teneral		Non-teneral	
Week	Males	Females	Males	Females
1	214	223	1061	968
2	160	158	240	427
3	151	284	152	229
4	165	183	68	146
5	220	207	55	106
6	215	203	59	102
7	234	178	84	88
8	266	217	39	72
9	209	163	45	70
10	218	151	32	56
11	142	114	34	66
12	110	96	17	73
13	90	50	28	41
14	59	39	22	23
15	67	40	17	21
16	52	33	23	26
17	47	23	11	19
18	45	24	15	20
19	27	25	13	26
20	44	21	12	27
21	25	27	12	11
22	24	11	11	6
23	32	39	6	26

Whiteside (1949) attacked tsetse-flies by introducing into their environment cattle externally treated with an insecticide. He notes that in principle the measure is similar to hand-catching, and that 'Successive weekly catches...differ insignificantly from a geometrical progression'.

Symes & Southby (1938) attacked tsetse-flies by hand-catching. They found that catches in successive months decreased in a geometrical progression.

Thus, all the examples which have been discovered in the literature confirm the theoretical conclusion reached in the earlier section, that the reduction of an animal population by artificial predation would proceed in a geometrical progression. None of the examples show the disturbances which might be expected owing to the intervention of control factors, or the various other possibilities envisaged, but this may well be because none of them proceeded all the way to extinction.

EXPERIMENTS ON ARTIFICIAL PREDATION OF TSETSE-FLIES

When a population of tsetse-flies is subjected to artificial predation, the postulate that the catches, and the population, will decrease in a geometrical progression must be modified, for the following reason. Tsetses do not have any particular breeding season, they breed throughout the year. Females deposit full-grown larvae on the surface of the soil: these burrow into the soil and at once pupate. The period spent as a pupa varies from 20 to 60 days according to the temperature, and the birth-rate and death-rate per week is often as high as 30%, at least for males.

Consider now an imaginary population of tsetse-flies containing 1000 adult (non-teneral) females. Suppose that 200 emerge and 200 die each week and that the temperature is such that the pupal period is 6 weeks. Now introduce artificial predation of an intensity that destroys one-quarter of the population per week. Ignoring for the

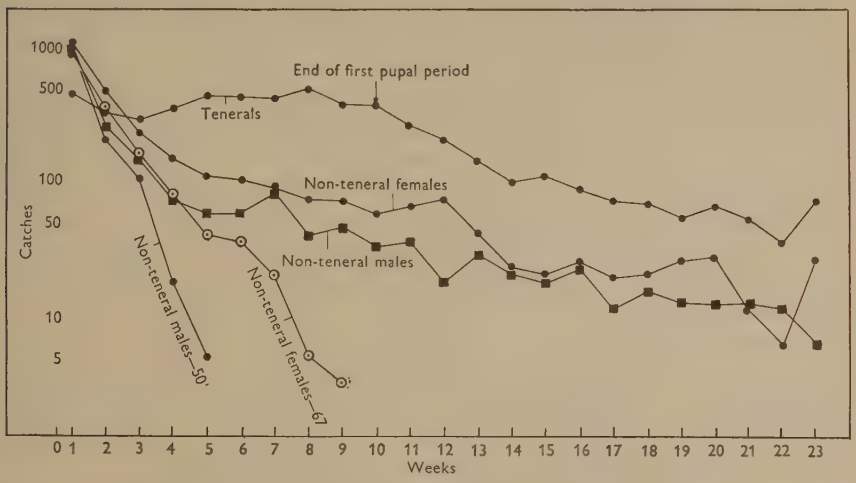

Fig. 1. Weekly catches of *Glossina palpalis* in Block VII from 15 July 1946

moment the birth-rate and normal deaths, the population at the end of each of the first 6 weeks would be: 750, 563, 422, 317, 237 and 178. But since the pupae stay in the soil for 6 weeks, emergences in the sixth week will still be from pupae deposited the week before artificial predation began, and will be at the old value of 200 per week. Normal deaths, however, in so far as they are not anticipated by artificial predation, will be at the rate of one-fifth of the current population per week. It is therefore impossible that the population will be reduced to as little as 178 at the end of the sixth week. In fact the population will fall rapidly for the first 3 weeks but will stabilize at about 300 in the second 3 weeks. In the seventh, eighth and ninth weeks there will be a rapid fall, followed by another stable period in the tenth, eleventh and twelfth weeks. This process will in theory continue indefinitely.

A population of tsetse (*Glossina palpalis fuscipes* Newstead) has been attacked by artificial predation. The practical aspects of this experiment, as a method of tsetse reclamation, have been described elsewhere (Glasgow & Duffy 1951). Some 45 catchers worked a strip of riverine forest, just over two miles long, on the banks of

a permanent stream. The catches in the first 23 weeks are given in Table 1 and Fig. 1. The graph is plotted on a logarithmic scale, because this converts curves of geometrical series into straight lines. The following points emerge from the examination of the graph:

(*a*) The catch of tenerals (total of both sexes) remained nearly constant for the first 10 weeks, after which it declined steadily. This implies that the pupal period was 9 weeks, which is not unreasonable, as the forest soil temperatures were fairly low.

(*b*) The catch of non-teneral females declined rapidly at first, but tended to stabilize at about 67 per week.

(*c*) Likewise, the catch of non-teneral males declined rapidly at first, but tended to stabilize at about 50 per week.

The steady catch of 67 non-teneral females per week, in the presence of a steady high catch of tenerals (mean 183 per week in the first 10 weeks) suggests that the original population was exterminated by about the eighth week, and that 67 per week was the number which eluded the catchers and managed to find a safe feed and so to become non-teneral. This would have been going on since the first week; therefore, if we subtract 67 from the catch of non-teneral females in each of the first 9 weeks, we obtain the series 901, 360, 162, 79, 39, 35, 21, 5 and 3, the sum of which, 1605, corresponds to the initial population of non-teneral females. (This argument assumes that none died of natural causes: a correction for this is introduced in the next section.) As shown in Fig. 1, the logarithms of this series and of the series (non-teneral males minus 50) lie near to straight lines, indicating that they approximate to geometrical series. The slope of the line corresponds to a value of f, the fraction caught per week, of 0·56. Since the mean catch of teneral females for the first 10 weeks was 183, and we have reason to believe that 67 tenerals per week eluded the catchers, evidently some 250 tenerals emerged each week. The catch of 183 corresponds to a value of $f = 0{\cdot}73$, i.e. teneral females are more easily caught than non-tenerals. It is not known why this is so, but it is a common observation with several species of *Glossina*.

ESTIMATE OF THE PREY POPULATION

The sum of the series (non-teneral females minus 67) is 1605. This is evidently the lower limit of the initial population. The true value would be 1605 plus the number which died natural deaths. The emergence of 250 teneral females per week corresponds to a birth-rate of 15·6% per week, and provided the population was steady before the experiment began, the death-rate would have been the same. As the death-rate due to our artificial predation was 56% per week, it seems probable that the natural death-rate was negligible. It may be, however, that it was not. If we assume that 15·6% per week of the remainder continued to die of natural causes, in addition to those killed by artificial predation, the initial population would be $1605 + 15{\cdot}6\% = 1855$, and this is evidently the upper limit of the initial population.

Similar reasoning applies to the non-teneral males. The catch stabilized at about 50 per week, and the graph of the logarithm of (non-teneral males minus 50) is shown in Fig. 1. In this case $f = 0{\cdot}76$. The mean catch of teneral males during the first 10 weeks was 203, so that $203 + 50 = 253$ males emerged each week. This is nearly equal to the numbers of females emerging (250 per week) as is usual (Jackson 1949). The catch of

203 per week corresponds to $f = 0{\cdot}80$, practically the same as the value found for non-teneral males (0·76). The sum of this series (non-teneral males minus 50) is 1326, which is the lower limit of the initial population. The emergence of 253 males per week corresponds to a birth-rate (and hence death-rate) of 19·1% per week. The upper limit of the initial population would thus be 1579. The reason why higher values of f have been found for males than for females is the well-known difference of behaviour between the sexes. Females are 'active', i.e. come to man only when they are in need

Table 2. *Marking and recapture of* Glossina palpalis *in Block VII, Kuja River, from 16 May to 10 July 1946*

MALES

Half-week of marking

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16		
306	42	119	83	110	77	57	51	27	24	56	42	37	32	14	21	242	
536	73	88	87	72	54	52	26	32	28	40	29	25	13	22		212	
496	40	66	55	61	40	26	33	42	18	26	23	31	26			231	
501	36	38	32	53	14	28	40	26	7	21	15	27				256	
466	20	29	36	20	22	22	25	21	13	16	17					280	
384	17	25	15	25	34	22	21	13	16	21						370	
331	11	17	12	38	17	26	11	17	13							292	
352	6	19	15	21	16	16	16	11								200	
187	8	15	13	11	9	17	12									363	
271	8	4	5	11	14	6										347	
357	9	5	12	8	9											401	
265	4	3	10	9												489	
244	1	2	7													523	
221	2	5														529	
204	3															572	
228																319	

Captures

Releases

FEMALES

Half-week of marking

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16		
219	15	39	15	44	25	23	12	18	16	22	15	8	4	5	5	94	
313	15	22	25	20	16	13	11	11	8	14	6	4	5	4		105	
286	16	26	21	15	19	9	13	11	7	7	1	7	5			110	
277	7	24	13	9	18	13	11	11	1	4	1	7				127	
314	6	11	7	13	20	3	3	9	1	5	4					184	
253	6	12	12	12	14	8	4	4	2	7						206	
189	3	4	7	8	8	5	0	11	3							253	
195	1	9	4	9	4	3	3	3								189	
174	7	5	3	4	4	3	1									204	
238	2	8	3	5	4	2										222	
192	1	6	2	3	3											270	
172	2	2	1	3												341	
113	1	0	1													313	
98	0	2														317	
99	1															343	
79																232	

Captures

Releases

of food. At other times, they are resting in various situations where they can only be found with so much trouble that in practice they must be regarded as non-available. Males, on the other hand, become active long before they are urgently hungry. They then come to man, not primarily to feed, but presumably in search of mates. Since teneral males are impotent, it was expected that the behaviour of teneral males and females would be the same; but the data considered here suggest that the teneral male anticipates its non-teneral behaviour.

It is of interest to compare the values given above, made by as near an approach to a direct count as probably could ever be reached with a wild tsetse population, with estimates of the population made by the methods of Jackson (1948). Before the catching-out work began, flies were marked and released every day except Sundays. The marks were changed twice a week, and the results, grouped into half-weeks, are given in

Table 2. Jackson used to mark on only three days a week, leaving a whole week interval between marking and first recapture. The reason for marking six days a week in the present instance was that it was desired at the same time to ascertain whether the experimental block of forest was in fact isolated. As none of the very considerable number of flies recorded as marked in Table 2 was ever recaptured outside of the experimental block, it was concluded that the block was adequately isolated, although it was later discovered that this was not so. Marking was done for $8\frac{1}{2}$ weeks immediately before the catching-out began. In the last three days, however, a large number of labourers were working in the block cutting paths and otherwise preparing for the catching-out. This so disturbed the flies that very few were caught and recaptures were anomalous. The seventeenth half-week is accordingly omitted from Table 2.

Before considering the population estimates made from the recaptures of marked flies, it is necessary first to pay attention to an unavoidable error in the marking procedure. Jackson points out that either the marking or the recapturing, or both, should be done by parties moving at random within the area being studied. However, while random movement is possible in the habitat of the savannah tsetses studied by Jackson,

Table 3. *Captures of non-teneral flies in the eighteenth half-week*

	Marked	Unmarked	Total
MALES			
North bank	144 (58 %)	105	249
South bank	215 (46 %)	251	466
Totals	359 (50 %)	356	715
FEMALES			
North bank	81 (41 %)	116	197
South bank	127 (41 %)	180	307
Totals	208	296	504

The proportion of marked males is significantly higher on the North bank, P being less than 0·01.

it is not possible in riverine forest, and in the present study the marking parties were obliged to keep to prepared paths. Previous experience had shown that the largest catches were made from paths following the edge of the river as closely as possible; this and other evidence suggested that hungry flies always sought the river, and it was therefore believed that a catch made from a riverside path gave an adequate and unbiased sample of the population, and no reason for altering this belief has been found. Two marking parties worked each day. The original intention was to have one party on each bank, but because of floods both parties in fact worked on the south bank. Each day one party started at the upstream end of the block and the other at the downstream end; each party worked right through the whole length of the block to finish at the point where the other party began. As the stream is only about 50 yards wide, it was believed that having both parties on the south bank did not matter. However, in the first half-week of catching out, it was found that while marked females appeared to be evenly dispersed on both banks, marked males were proportionally more numerous on the north bank (i.e. the bank on which no marking had been done). The data are presented in Table 3. The discovery of a greater proportion of marked males on the north bank was quite unexpected, and no satisfactory explanation has been suggested. It is clear, however, that the population estimate based on recaptures on the south bank only will be too high, because the number of recaptures was depressed.

Table 4 gives the 'corrected recaptures', i.e. the actual recaptures corrected to their theoretical value, had only 100 flies been released in the half-week of marking and 100 caught in the half-week of recapture. Since the teneral flies are marked in their first period of activity, they count as releases but not as captures, no recaptures ever

Table 4. *Corrected recaptures of* Glossina palpalis (*see Table 2*)

MALES — Half-week of marking

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
2·5	4·2	3·1	4·5	4·1	4·3	4·2	4·0	4·4	5·4	4·3	5·4	5·7	3·0	4·4	
4·6	3·1	3·5	3·6	3·3	3·7	4·0	3·3	3·9	5·2	3·2	4·0	2·5	4·2		
2·5	2·5	2·7	3·5	2·3	3·5	3·5	3·2	3·4	3·7	2·8	5·4	4·5			
2·4	1·7	1·8	2·9	1·5	2·6	3·2	2·7	1·4	3·3	2·0	4·2				
1·6	1·5	1·9	2·1	1·7	1·5	2·7	2·4	2·9	2·7	2·0					
1·6	1·2	1·5	1·8	2·0	2·1	2·5	1·6	3·9	3·2						
1·0	1·6	0·8	2·0	1·3	2·7	1·4	2·3	2·9							
1·0	1·2	0·8	1·5	1·3	1·8	2·3	1·3								
0·9	0·7	0·9	0·9	0·8	2·1	1·5									
0·7	0·3	0·4	1·0	1·4	0·7										
1·1	0·4	1·0	0·8	0·8											
0·5	0·2	0·9	0·8												
0·1	0·2	0·6													
0·3	0·4														
0·4															

FEMALES — Half-week of marking

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
2·1	4·0	1·7	4·5	2·9	4·5	2·8	5·1	3·6	4·5	4·2	3·8	3·2	4·6	6·0	
2·3	2·3	2·5	2·5	2·5	2·5	2·8	2·3	2·2	3·2	2·6	2·2	4·0	4·6		
2·5	2·4	2·6	2·5	2·9	1·9	2·5	2·8	2·2	2·4	0·5	3·8	5·0			
1·0	2·8	2·2	1·5	3·0	2·0	2·6	3·1	0·5	1·6	0·5	4·8				
1·0	1·7	1·1	2·4	2·5	0·6	0·8	3·9	0·5	2·0	2·5					
1·4	1·8	2·2	1·6	2·1	1·7	1·6	2·0	1·1	3·5						
0·7	0·7	0·9	1·3	1·4	1·6	0·0	5·4	2·0							
0·2	1·1	0·7	1·7	1·0	1·1	1·4	1·9								
1·3	0·8	0·6	1·1	1·2	1·1	0·8									
0·5	1·4	0·8	1·6	1·2	0·9										
0·3	1·5	0·6	1·0	1·1											
0·8	0·6	0·3	1·2												
0·4	0·0	0·4													
0·0	0·7														
0·5															

being teneral. The top left-hand figure of Table 4 (the corrected recapture in the second half-week of males marked one half-week previously) is calculated from the data of Table 2 as follows:

$$\frac{42 \times 10{,}000}{519 \times 536} = 2{\cdot}5.$$

The method used for calculating the populations and birth-rates are essentially those given by Jackson (1948). In a recent departmental report, however, Dr Jackson has produced improvements which enable the data to be displayed in a 'Fisher Lattice' (Tables 2 and 4) and which use all the data.

Dates:

a	*b*	*c*	*d*	*e*	*f*
C_a	A_1	B_1	C_1	D_1	E_1	C'_f
C_b	A_2	B_2	C_2	D_2	C'_e
C_c	A_3	B_3	C_3	C'_d
C_d	A_4	B_4	C'_c
C_e	A_5	C'_b
C_f	C'_a

Here C_a, C_b, etc., are the number caught (including recaptures) on the respective dates of capture, and C'_a, C'_b are the numbers released on those dates.

The corrected recapture figures are then worked out on a double percentage basis to allow for the fact that numbers marked vary from date to date:

$$a_1 = A_1 \frac{100}{C'_a} \times \frac{100}{C_b}; \quad a_2 = A_2 \frac{100}{C'_a} \times \frac{100}{C_c}; \quad \text{etc.}$$

Dates:	a	b	c	d	e	f
	a_1	b_1	c_1	d_1	e_1	
	a_2	b_2	c_2	d_2		
	a_3	b_3	c_3			
	a_4	b_4				
	a_5					

Here of course C_a (not shown) $= C'_a = C_b$, ..., etc. $= 100$.

Since a_2 stands in the same ratio to b_1 as does a_1 to the unknown value b (the date of release being the only difference in each case), and since the same applies to the whole respective series a and b which differ only in their marking dates, the extrapolated points b_0, c_0, etc., are calculated:

$$\left.\begin{aligned} b_0 &= a_1 \frac{b_1 + b_2 + b_3 + \ldots}{a_2 + a_3 + a_4 + \ldots}, \\ c_0 &= b_1 \frac{c_1 + c_2 + c_3 + \ldots}{b_2 + b_3 + b_4 + \ldots}, \end{aligned}\right\} \qquad (1)$$

or alternatively:

$$e_0 = e_1 \frac{d_1 + c_2 + b_3 + \ldots}{d_2 + c_3 + b_4 + \ldots}. \qquad (2)$$

The fractions of the form $\frac{b_1 + b_2 + b_3 + b_4}{a_2 + a_3 + a_4 + a_5}$ are the reciprocals of Jackson's r_-, and the fractions of the form $\frac{d_1 + c_2 + b_3 + a_4}{d_2 + c_3 + b_4 + a_5}$ are the reciprocals of Jackson's r_+.

The death-emigration rate for the period a–b is $1 - r_-$, and the birth-immigration rate for the period e–f is $1 - r_+$. Weighted means of r are best made by adding all the numerators and then all the denominators of the individual values of r.

The population is calculated by dividing the extrapolated point (a_0, b_0, etc.) into 10,000. Means of population estimates are best found by first taking means of extrapolated points.

The variance of any value of r is $\frac{r + r^2}{R_1 + \ldots + R_k}$, where R_1, ..., R_k are the uncorrected recaptures from which the denominator of r was derived.

Table 5 gives the estimates of the population, birth-rate and death-rate, calculated by these methods from Table 4. Comparing these values with those previously found (p. 38), we see that in the case of the males, the birth-rate found by the marking method is on the high side, but the fiducial limits of the birth-rate found by the marking method comfortably embrace the value found by the artificial predation method. The population estimate is too high, as we predicted. Table 3 suggests that recaptures on the south bank were about 4% too low. Increasing the mean value of the extrapolated

Table 5. *The population and birth and death rates of* Glossina palpalis *in Block VII, Kuja River from 16 May to 10 July 1946 calculated from the data of Table 4*

(The column headed a_1/r_- gives the extrapolated points calculated from formula (1); P_- are the corresponding population estimates. That headed e_1/r_+ gives the extrapolated points calculated from formula (2).)

MALES

Half week	r_- Numerator	r_- Denominator	$\frac{a_1}{r_-}$	P_-	r_+ Numerator	r_+ Denominator	$\frac{e_1}{r_+}$	P_+
1	—	—	—	—	—	—	—	—
2	18·7	19·2	2·57	3890	4·6	2·5	2·27	4400
3	15·0	19·9	5·57	1800	5·6	8·8	4·87	2050
4	16·8	25·4	4·66	2150	8·4	8·6	4·59	2180
5	20·9	20·5	4·41	2270	9·6	12·9	5·49	1820
6	16·4	25·0	6·25	1600	11·7	13·7	5·03	1990
7	20·7	25·3	5·28	1890	13·0	16·0	5·17	1930
8	21·1	20·8	4·14	2420	15·2	17·2	4·52	2210
9	16·8	22·8	5·43	1849	15·8	19·2	5·37	1860
10	18·4	23·5	5·62	1780	18·0	20·2	6·05	1650
11	18·1	14·3	3·48	2870	21·2	23·4	4·73	2110
12	10·0	19·0	8·17	1220	19·4	25·5	7·07	1410
13	13·6	12·7	5·04	1980	20·9	24·8	6·78	1470
14	7·0	7·2	5·86	1710	26·8	26·6	2·97	3370
15	4·2	4·4	3·14	3190	27·5	29·8	4·75	2100
16	—	—	—	—	—	—	—	—
Totals	217·7	260·0	—	—	217·7	249·2	—	—
Means	—	—	4·97	2010	—	—	4·98	2008

FEMALES

1	—	—	—	—	—	—	—	—
2	12·9	21·8	3·55	2820	2·3	2·1	3·64	2750
3	17·8	16·6	3·73	2680	4·8	6·3	2·24	4460
4	14·9	22·9	2·61	3830	5·9	6·5	4·95	2020
5	18·4	21·8	5·33	1880	8·9	10·4	3·36	2980
6	18·9	17·9	2·75	3640	10·3	11·8	5·18	1930
7	13·4	15·3	5·14	1950	10·5	14·8	3·95	2532
8	12·5	26·5	5·94	1680	13·2	13·3	5·15	1940
9	21·4	12·1	2·88	3470	14·2	18·3	4·61	2170
10	8·5	17·2	7·28	1370	13·6	17·8	5·94	1680
11	12·7	10·3	3·65	2740	16·4	18·1	4·62	2165
12	6·1	14·6	10·05	995	17·8	20·6	4·41	2270
13	10·8	12·2	4·29	2330	12·3	21·6	5·60	1790
14	9·0	9·2	3·27	3060	21·8	15·5	3·27	3060
15	4·6	6·0	6·00	1667	29·9	26·4	5·34	1870
16	—	—	—	—	—	—	—	—
Totals	181·9	224·4	—	—	181·9	203·5	—	—
Means	—	—	4·75	2105	—	—	4·45	2247

	Males	Females
Mean value of r_-	0·8373	0·8106
Corresponding death-rate (%)	16	19
Mean value of r_+	0·8736	0·8939
Corresponding birth-rate (%)	13	11
Standard error of r_+	0·02335	0·04029
r_+ + twice S.E.	0·9203	0·9745
r_+ − twice S.E.	0·8269	0·8133
Corresponding birth-rates (%)	8–17	3–19
Weekly birth-rate, $1-r_+^2$ (%)	24	20
Weekly birth-rate with fiducial limits (%)	16–31	5–34

point, 4·98, by 4%, we get 5·18; the corresponding population estimate is 1930. In view of the range of values in the P_+ column of Table 5, it will not be contended that this is significantly greater than the value obtained by the artificial predation method. In the case of the females, both birth-rate and population as estimated by the marking method are on the high side as compared with the estimate by the artificial predation method, but again, not impossibly high. Table 6 summarizes and compares the findings. The birth-rate found by either method, and the death-rate found by the marking method, should strictly speaking be referred to as rates of 'birth-immigration' and 'death-emigration'. Later on it was possible to make an estimate of the immigration rate, from which it appeared that the element of immigration in the initial 'birth-immigration' rate was very small.

Table 6. *Populations and birth-rates of non-teneral flies estimated by two methods*

	Males		Females	
	Population	Weekly birth-rate (%)	Population	Weekly birth-rate (%)
Artificial predation	1326–1579	19·1	1605–1855	15·6
Marking	1930	16–31	2170	5–34

Table 7. *Release and recapture of marked foreign non-teneral males in Block VII Kuja River from 28 February to 16 April 1949*

ACTUAL FIGURES

Weeks	1	2	3	4	5	6	7	
Releases	14	24	32	17	36	47		
	38	3	7	2	1	0	158	
	49	0	0	0	0	167		
	79	1	0	0	168			
	52	8	0	126				
	77	0	104					
	76	71						
Captures								

CORRECTED FIGURES

Weeks	1	2	3	4	5	6	7
Releases	51·9	47·1	32·2	19·5	28·0	39·1	
	8·4	8·5	3·1	0·8	0·0		
	0·0	0·0	0·0	0·0			
	2·7	0·0	0·0				
	14·6	0·0					
	0·0						
Captures							

Week	r_- Numerator	r_- Denominator	$\frac{a_1}{r_-}$	P_-	r_+ Numerator	r_+ Denominator	$\frac{e_1}{r_+}$	P_+
1	—	—	—	—	—	—	—	—
2	25·7	55·6	112·3	89	0	43·4	—	—
3	8·5	35·3	195·6	51	15·4	25·3	46·0	22
4	3·1	20·3	210·9	47	5·8	40·7	136·8	73
5	0·8	28·0	682·5	15	8·5	55·5	210·2	48
6	0·0	39·1	—	—	8·4	51·9	291·0	34
7	—	—	—	—	—	—	—	—
Totals	38·1	178·3	—	—	38·1	173·4	—	—
Means	—	—	300·3	33	—	—	171·0	58

$r_-=0·21$; $r_+=0·22$; death-rate = 79%; birth-rate = 78%; mean population = 42.

The immigration was estimated in the following way. The catching out, which had begun with such promise (Table 1), reached a stage in which the weekly catch stabilized and could not be reduced any more. In February 1949 the mean catch of non-teneral males was 25 per week. Male *G. palpalis* were now caught every day in the control block, where they were numerous, marked, and released in Block VII. The releasing was done at dusk, after the catchers had stopped work for the day. The details are given in Table 7. Some marked flies were recaptured in the same week as that in

which they were released. Since such flies were not available for recapture in subsequent weeks, they are excluded from the table. The calculations of the population, birth-rate and death-rate are also given. It is clear that the mean population, 42, includes a number of foreign marked flies. We see from Table 7 that during the period of the operation 371 male *G. palpalis* were caught, of which 192 were marked and 179 were not. The indigenous population was therefore $42 \times 179/371 = 20$. The birth-immigration rate was 78% or 16 non-teneral males per week. Since the true birth-rate is about 20% per week, as we saw above, it is clear that about 12 of the 16 were immigrants. This rate of immigration would be enough to account for the failure of the hand-catching operation. On the other hand, it would make very little difference to the estimates of the birth-rate at the beginning of the experiment in 1946. Thus, if the total emergence of males was 241 instead of 253 per week, the male birth-rate was 18·2% instead of 19·1%. The immigrants would reduce the marking estimate of the birth-rate by a similar amount.

ACKNOWLEDGEMENTS

I am much indebted to various of my colleagues: especially to Mr B. J. Duffy who was in charge of the Block VII hand-catching experiment. Dr C. H. N. Jackson and Mr E. F. Whiteside have been untiring correspondents, and the latter suggested the ingenious method of estimating a very small population by introducing marked foreign male flies.

SUMMARY

1. Artificial predation is defined as a predator-prey relationship in which the predator is man. Examples from the literature are given in which artificial predation was successful, in the sense that the prey species was exterminated or nearly so, and other examples in which it was unsuccessful.

2. It is shown on theoretical grounds that reduction of a prey population by means of artificial predation would be expected to follow a geometrical progression; in several examples from the literature this expectation is fulfilled.

3. In an experiment in which a population of tsetse flies was subjected to artificial predation the geometrical expectation was fulfilled closely.

4. In this same experiment, by summing the geometric series, it was possible to estimate the initial prey population and birth-rate of tsetses. These estimates agreed well with independent estimates made before the start of artificial predation by the method of releasing and recapturing marked flies.

5. The element of immigration, included in the birth-rate in both methods of estimation, was shown to have a low numerical value which was negligible when the population was large, as at the beginning of the experiment, but was big enough to prevent the artificial predation proceeding to extermination.

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A CENSUS OF THE TSETSE-FLY *GLOSSINA PALLIDIPES* AUSTEN AND OF ITS HOST ANIMALS

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(With 2 Figures in the Text)

INTRODUCTION

During observations directed primarily towards the waterside tsetse, *Glossina palpalis fuscipes* Newstead, high apparent densities of *G. pallidipes* Austen were noticed. Interest was aroused because possible host animals for *G. pallidipes* were rather rare, and this paper reports a simultaneous census of the tsetses and of their hosts.

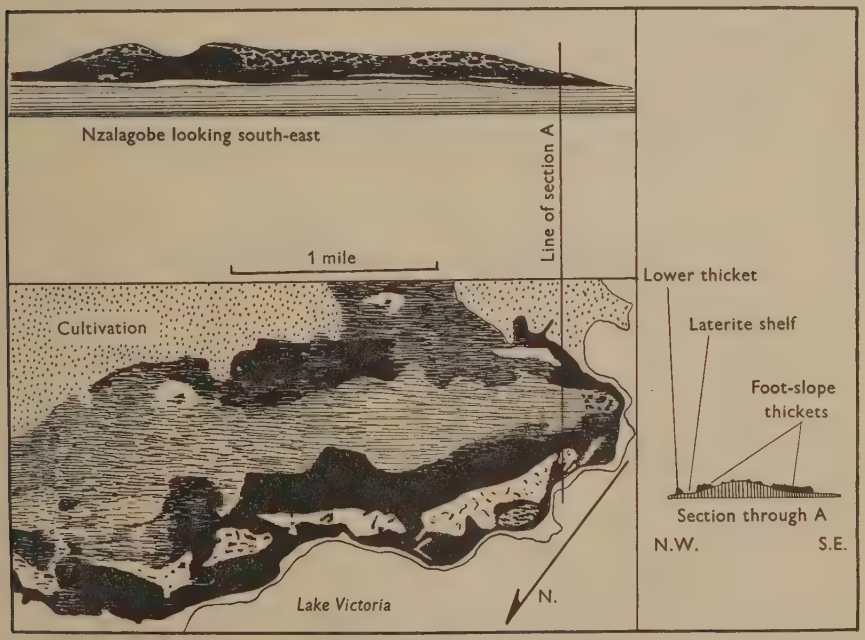
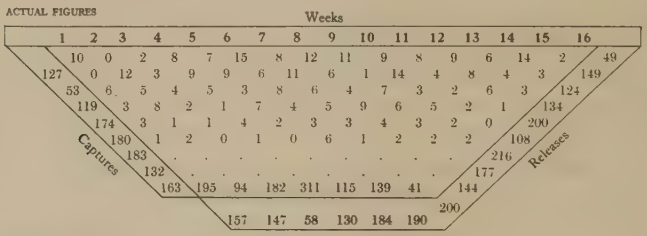


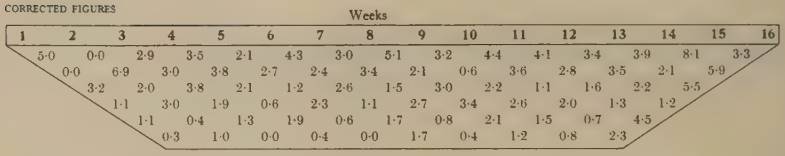
Fig. 1. Nzalagobe.

The scene of the observations was Nzalagobe hill, lat. 0° 7′ N., long. 34° E. This is a ridge the top of which is about 500 ft. above the level of Lake Victoria. It runs roughly N.E.–S.W., the N.W. flank and the S.W. end being bounded by the waters of Berkeley Bay. The top and steep slopes of the ridge are lightly wooded with low thickets and glades, but on each side below the steep slopes is a well-developed foot-slope thicket (Fig. 1). This is a narrow zone of solid thicket 25–30 ft. high. On the N.W. slope, below the foot-slope thicket, is a shelf of laterite rock, which carries very

little soil and very little vegetation. Below the laterite shelf is another zone of thicket, similar to the foot-slope thicket, and apparently owing its distinctive character to run-off from the laterite, just as the foot-slope thicket presumably depends on run-off from the steep stony slopes above it. Below this lower thicket zone there was originally the narrow lake-side forest, but this had been removed in 1947 and replaced by grassland,

Table 1. *Marking and recapture of male* Glossina palpalis *on Nzalagobe from 3 May to 18 July 1950*





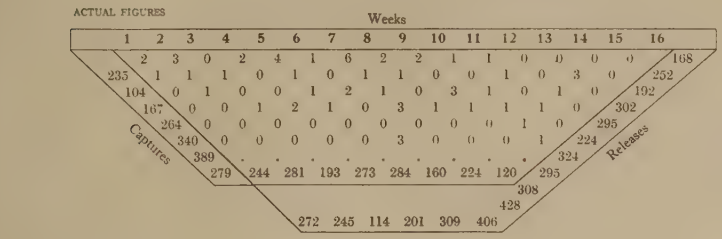
Week	r_- Numerator	r_- Denominator	$\frac{a_1}{r_-}$	r_+ Numerator	r_+ Denominator	$\frac{e_1}{r_+}$
1	—	—	—	—	—	—
2	5·7	13·3	1·17	0·0	5·0	—
3	13·3	12·9	—	10·1	0·0	—
4	10·0	12·3	3·57	6·1	13·0	8·31
5	8·8	8·9	3·45	11·7	9·6	2·79
6	6·8	13·8	4·26	7·4	13·8	7·65
7	9·5	11·8	5·34	6·5	11·7	7·92
8	8·8	16·9	5·76	10·2	9·5	2·98
9	11·8	10·9	4·71	5·7	15·3	13·69
10	7·7	14·1	5·86	8·0	8·9	3·34
11	9·7	14·3	6·49	11·7	12·4	4·56
12	10·2	10·3	4·10	9·0	15·8	3·69
13	6·9	11·5	5·67	9·8	12·4	4·43
14	7·6	14·0	7·18	7·1	13·7	5·60
15	5·9	3·3	4·53	19·4	15·2	—
16	—	—	—	—	—	—
Totals	122·7	168·3	62·18	122·7	156·3	64·96

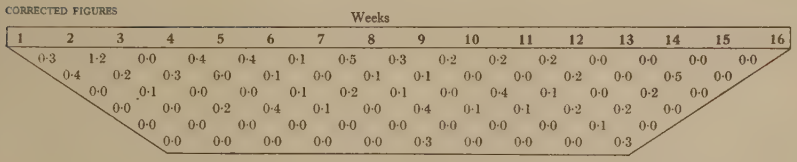
$r_- = 0{\cdot}73$; $r_+ = 0{\cdot}79$; death-rate = 27 % per week; birth-rate = 21 % per week. Mean extrapolated point: 5·298; mean population: 1892 non-teneral males; probable total population: 5000.

in an attempted experimental eradication of *G. palpalis*. This measure, however, had not eradicated *G. palpalis*, which continued to live, although in reduced numbers, in the thicket zones already described. On the S.E. slope of the ridge there is another foot-slope thicket, but on this side there is but little laterite shelf, and consequently only one thicket zone. The coast was described by Carpenter (1924) and by Symes & Southby (1938). It is clear that Nzalagobe has been uninhabited since before 1924.

Traces of native iron workings are frequent in the foot-slope thickets, but these workings have been abandoned, according to local testimony, for some forty years. As a consequence of this former occupation, however, a very common element in the foot-slope thickets is *Euphorbia tircualli* L., a tree often used for live fences round native compounds.

Table 2. *Marking and recapture of male* Glossina pallidipes *on Nzalagobe, 3 May to 18 July 1950*





Week	r_- Numerator	r_- Denominator	$\frac{a_1}{r_-}$	r_+ Numerator	r_+ Denominator	$\frac{e_1}{r_+}$
1	—	—	—	—	—	—
2	0·4	1·5	1·13	0·4	0·3	0·90
3	0·3	0·5	2·00	0·2	1·6	—
4	0·5	0·8	—	0·4	0·2	0·20
5	0·4	0·7	0·70	0·0	0·8	—
6	0·3	0·6	0·80	0·3	0·4	0·13
7	0·5	1·1	0·22	0·5	0·4	0·40
8	0·6	0·5	0·43	0·4	1·0	0·75
9	0·2	0·7	1·05	0·2	0·7	0·70
10	0·5	0·9	0·36	0·4	0·4	0·20
11	0·7	0·6	0·17	0·8	0·6	0·15
12	0·4	0·2	0·10	0·4	1·0	—
13	0·2	0·5	—	0·2	0·4	—
14	0·5	0·0	—	1·0	0·2	—
15	0·0	0·0	—	0·3	1·0	—
16	—	—	—	—	—	—
Totals	5·5	8·6	6·96	5·5	9·0	3·43

$r_-=0{\cdot}64$; $r_+=0{\cdot}61$; death-rate = 36 % per week; birth-rate = 39 % per week. Mean extrapolated point: 0·5772; population: 17,325 non-teneral males; probable total population: 50,000.

Glossina pallidipes is virtually confined to the foot-slope thickets, including the lower thicket on the N.W. slope. The tongue of thicket running off to the south of the ridge is unsuitable for tsetses, so that as far as the two species of tsetse are concerned Nzalagobe is a peninsula bounded by the lake to the N.W., and elsewhere by native cultivation, and joined to the main land only by a narrow isthmus at the N.E. end of

the ridge. The same factors tend to confine the mammals to Nzalagobe. It is thus reasonable to treat Nzalagobe as a separate entity, although it is not strictly isolated.

CENSUS OF TSETSES

Paths were cut along the whole length of all the foot-slope thickets, keeping as far as possible to the middle of the strips of thicket. Since the foot-slope thickets were quite narrow strips, to which the tsetses were confined, catches made on these paths gave an adequate sample of the tsetse population. This was certainly so of *G. palpalis*; in the case of *G. pallidipes*, the bush leading up to the wooded saddle, shown in Fig. 1 near the left-hand end of Nzalagobe, was perhaps not adequately sampled. This would mean that we were sampling a population less than the total population, so that our estimate of the tsetse population is, if anything, on the low side.

The paths through the foot-slope thickets had an aggregate length of 14,900 yards. *G. pallidipes* and *G. palpalis* were taken together in most places, but *G. palpalis* was commonest in the parts nearest the lake. Four separate parties working on different divisions of the paths marked, released and recaptured the flies during the first 3 days of 16 weeks, from 3 April to 20 July 1950. The results are presented in Tables 1 and 2. The calculations follow the methods of Jackson (1948) with the modifications explained by Glasgow (1953).

The estimate of the tsetse population is 1800 *G. palpalis* and 17,000 *G. pallidipes*. This refers to 'non-teneral' males, i.e. to those which have had at least one blood meal. The total population, including tenerals and females, would probably be at least three times the non-teneral male population, or in round figures 5000 *G. palpalis* and 50,000 *G. pallidipes*.

CENSUS OF MAMMALS

At the same time as the tsetse population estimates were being made, animal tracks were recorded on the same paths. For this work, local natives with an especial interest in game were engaged. Two strands of cotton at 12 and 24 in. from the ground were stretched along the up-hill sides of the paths. The ground was hoed, where necessary, to make it receptive to tracks. One tracker walked along each path every day except Sundays, recording on a form the species and number of animals, and the direction in which they crossed the path. The tracks were afterwards obliterated to avoid confusion next day.

The animals present were:

Bushbuck	*Tragelaphus scriptus* Pall.	Leopard	*Felis pardus* L.
Duiker	*Sylvicapra grimmia* L.	Hyena	*Crocuta crocuta* Erxleben.
Bushpig	*Potamochoerus porcus* L.	Hippopotamus	*Hippopotamus amphibius* L.
Waterbuck	*Kobus defassa* Ruppell	Buffalo	*Syncerus caffer* Sparrman.
Reedbuck	*Redunca redunca* Pall.		

Slight doubt attaches to the duiker, which is possibly a forest duiker, *Cephalophus* sp. We were unable to secure a specimen, but we think it probable that it was the common *Sylvicapra*. Other possible hosts of tsetse which we were unable to take into account were crocodile (*Crocodilus niloticus*), varanus (*Varanus* sp.), monkey (*Cercopithecus aethiops* L.), and porcupine (*Hystrix* sp.). Crocodiles were rare during the period of the observations, owing to fairly intensive shooting. When present, they are important

o *Glossina palpalis*, but it is doubtful if they are ever of importance to *G. pallidipes*. Varanus were very seldom seen. These lizards normally seem to be almost as closely associated with the water as crocodiles are, but one large one was several times seen basking on the road near the N.E. end of Nzalagobe. This spot is a mile from the lake, and possibly this varanus belonged to the terrestrial species. Porcupines were not common, but were recorded on one occasion as having broken the thread fence. The common grey monkey of the lake side was very common, and often broke the threads.

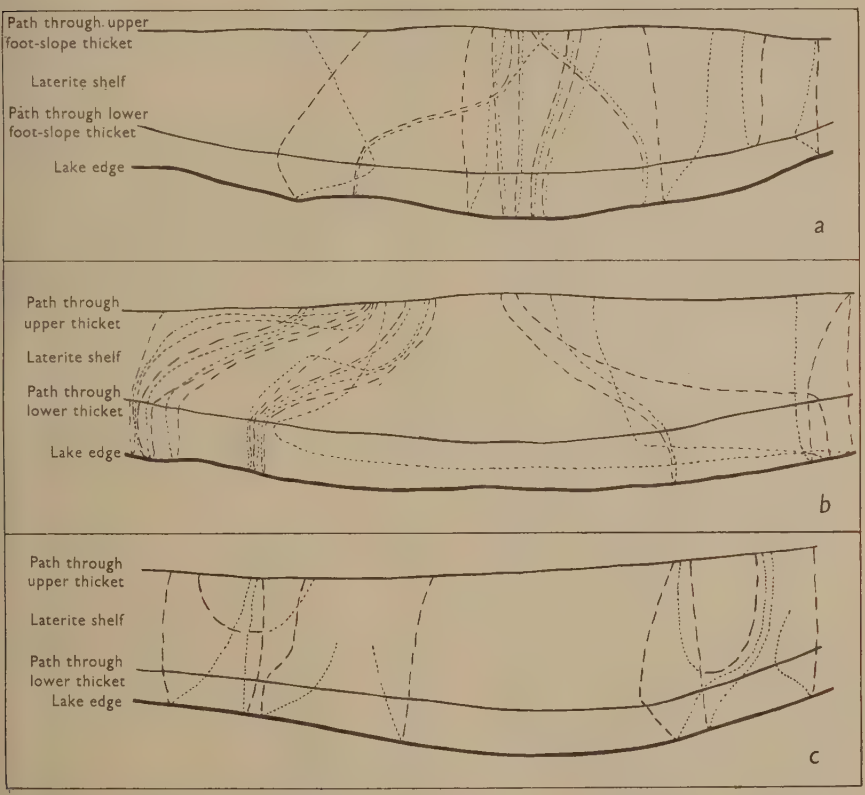


Fig. 2. Tracks of (*a*) bushbuck, (*b*) bushpig, and (*c*) duiker. – – –, downward; · · · · ·, upward tracks.

The tracking gives no indication of their numbers, but our impression is that they were more numerous than all other animals put together.

Daily observations of tracks were made for 9 weeks. After this, an attempt was made to track individual animals. The trackers were sent along the path through the upper thicket on the N.W. slope, with instructions to follow the first downward track they found. They did this only for the three commonest species, bushbuck, bushpig and duiker, for 2 weeks. The results of this individual tracking are shown in Fig. 2.

We now decided, from consideration of the results so far obtained, especially the tracking of individuals, that a reasonable estimate of the mammal population would

be obtained by assuming that during the day the animals lay up somewhere above our paths, and that they all came down to drink every night. (Hippopotami do the opposite: they spend the day in the water and come ashore to graze at night.) To complete the picture, another tracking path was installed running round the S.W. end of the hill to join the paths running through the thickets. The hill was now encircled by tracking paths, except for a gap across the N.E. end. This gap, however, was on the landward side and so could not be used by animals going to drink. Table 3 summarizes the

Table 3. *Tracks on Nzalagobe from 10 to 22 July 1950*

Date	Bushbuck	Bushpig	Duiker	Reed-buck	Water-buck	Hyena	Leopard	Hippo-potamus
UPWARD TRACKS								
10	13	21	6	0	1	0	2	1
11	13	11	5	3	0	1	1	2
12	14	16	5	2	0	0	1	2
13	11	18	4	3	1	1	1	0
14	8	12	4	1	0	0	1	3
15	14	12	4	1	0	2	1	3
Mean	12	15	5	2	0·3	0·7	1	2
Range	8–14	11–21	4–6	0–3	0–1	0–2	1–2	0–3
17	10	11	6	0	0	0	0	3
18	13	13	7	1	0	0	1	5
19	13	15	4	2	0	0	1	1
20	10	12	5	0	0	1	0	4
21	12	19	5	1	0	1	0	2
22	22	20	6	5	0	0	1	4
Mean	13	15	6	2	0	0·3	0·3	3
Range	10–22	11–20	4–7	0–5	0	0–1	0–1	1–5
DOWNWARD TRACKS								
10	11	16	6	0	0	0	1	2
11	9	8	3	1	0	1	1	2
12	9	20	1	2	0	0	1	2
13	14	7	3	1	1	1	0	0
14	9	12	6	1	0	0	1	4
15	10	13	6	1	0	0	0	4
Mean	10	13	4	1	0·2	0·3	0·7	2
Range	9–14	7–20	1–6	0–2	0–1	0–1	0–1	0–4
17	14	12	6	0	0	0	0	3
18	10	15	7	1	0	0	0	5
19	9	29	7	2	0	0	0	0
20	10	15	8	0	0	0	1	4
21	10	13	7	0	0	0	1	2
22	20	18	6	3	0	0	1	4
Mean	12	17	7	1	0	0	0·5	3
Range	9–20	12–29	6–8	0–3	0	0	0–1	0–5

In week 17–22 July hippopotami were tracked also along the lake edge. Those reaching the thicket path, as compared to those coming ashore, were 3/11, 5/10, 1/9, 4/5, 2/8, 4/13.

observations of upward and downward tracks. Tracks from the upper thicket on the N.W. slope are not included, as any animal crossing this thicket must also cross the lower thicket, below the laterite shelf, on its way to the water.

Table 4 gives the weekly means and ranges for the 9 weeks 17 April to 17 June 1950. These are included to show that moderately self-consistent results were obtained during 9 weeks. The actual estimates of the populations, however, are based on

Table 3, since the path round the end of the hill was operated only during the 2 weeks to which this table refers. It will be noticed that the hippopotamus records in Tables 3 and 4 are very irregular. This is because a herd of about thirty was living about the shores of Berkeley Bay. At night the herd broke up into small parties which went

Table 4. *Summary of tracks on Nzalagobe from 17 April to 17 June 1950, showing means and ranges by weeks*

	Bushbuck	Bushpig	Duiker	Reed-buck	Water-buck	Hyena	Leopard	Hippo-potamus	Buffalo
ARD TRACKS									
Mean	12·3	15·3	5·0	2·0	1·2	0·5	1·0	2·3	0·3
Range	7–18	10–24	4–7	1–4	1–2	0–1	0–2	1–4	0–1
Mean	8·7	15·0	3·5	1·3	0·5	0·3	0·3	1·5	0
Range	7–10	8–22	2–5	1–2	0–1	0–1	0–1	0–4	0
Mean	11·8	11·2	4·5	1·7	0·5	0	0·5	2·0	0
Range	7–21	7–15	3–6	1–3	0–1	0	0–1	0–5	0
Mean	9·7	10·0	3·2	0·7	0·5	0·3	0·3	3·8	0·3
Range	7–12	7–15	2–5	0–1	0–1	0–1	0–1	2–5	0–1
Mean	6·5	11·3	4·2	0·8	0·8	0·2	0·3	2·3	0
Range	5–8	9–15	3–5	0–2	0–2	0–1	0–1	2–3	0
Mean	11·2	12·8	5·2	2·0	0·8	0·2	0·6	3·0	0
Range	7–17	7–18	4–7	1–4	0–1	0–1	0–1	1–5	0
Mean	11·0	14·5	4·5	2·5	0·3	0·2	1·0	2·0	0·2
Range	9–14	5–21	3–8	1–3	0–1	0–1	0–3	0–6	0–1
Mean	10·8	9·2	3·8	1·0	0·2	0·2	0·2	3·8	0
Range	6–16	5–13	2–6	0–2	0–1	0–1	0–1	2–5	0
Mean	9·2	11·6	4·2	1·0	0·4	0	0·6	3·2	0
Range	6–12	8–14	4–5	1–1	0–1	0	0–2	1–5	0
NWARD TRACKS									
Mean	9·8	12·2	3·8	1·1	0·8	0·3	0·5	3·7	0·2
Range	7–16	8–16	2–5	1–2	0–2	0–1	0–1	1–8	0–1
Mean	6·8	14·5	3·2	1·0	0·3	0·2	0·5	1·5	0
Range	5–12	11–20	2–4	1–2	0–1	0–1	0–1	0–2	0
Mean	8·3	11·2	2·7	0·8	0·3	0	0·5	2·8	0
Range	5–12	8–16	1–4	0–2	0–1	0	0–1	0–7	0
Mean	6·7	10·0	2·5	0·3	0·3	0·2	0·2	3·2	0·3
Range	2–12	7–15	1–3	0–1	0–1	0–1	0–1	1–5	0–1
Mean	5·2	11·2	3·3	0·7	0·5	0·2	0·3	2·3	0
Range	2–7	6–16	2–4	0–1	0–1	0–1	0–1	2–3	0
Mean	7·8	12·8	3·4	1·4	0·8	0·4	0·6	2·8	0
Range	6–12	10–15	2–5	1–2	0–1	0–1	0–2	1–5	0
Mean	8·2	12·8	3·7	0·8	0·3	0	0·5	2·3	0
Range	5–10	10–17	2–5	0–2	0–2	0	0–1	0–6	0
Mean	11·2	11·0	4·6	0·6	0·6	0·4	0·4	4·1	0
Range	7–16	6–16	2–7	0–1	0–2	0–1	0–1	3–5	0
Mean	7·2	13·6	3·4	0·8	0·4	0·2	0·8	3·4	0
Range	5–11	9–20	2–6	0–2	0–1	0–1	0–2	1–5	0

ashore in widely different places. This was shown by cutting a tracking path along 7 miles of shore, northwards from a point a little way south of Nzalagobe. Table 5 summarizes the observations on this path. Naturally the number coming ashore each night on a relatively short piece of coast such as Nzalagobe varies considerably. Since

they are primarily grazing animals the majority of those that do come ashore on Nzalagobe stay in the narrow lake side clearing, where the grazing is excellent. Only a few eccentrics climb up into the bush, and their contact with the mainly diurnal *G. pallidipes* would be but slight.

The value of the thread fences is not clearly established. Besides being broken by the animals under study, the threads were sometimes broken by men, monkeys and porcupines. Sometimes the threads broke spontaneously, and this became common after they had been a month to 6 weeks exposed. On the other hand, some animals crossed the threads without breaking them. Table 6 summarizes the findings. There

Table 5. *Water-side hippopotamus tracks on 7 miles of shore*

(Greatest number observed, up or down)

25 July	24	31 July	27	7 Aug.	30	14 Aug.	20	21 Aug.	18
26	26	1 Aug.	30	8	20	16	29	22	22
27	13	2	17	9	17	17	28	23	15
28	21	3	23	10	25	18	22	24	24
29	17	4	19	11	24	19	14	25	19
Mean	20·2	5	22	12	20	Mean	22·6	26	19
Range	13–26	Mean	32·0	Mean	22·7	Range	14–29	Mean	19
		Range	17–30	Range	17–30			Range	18

seems to be something wrong with these figures, since it is difficult to imagine a hippopotamus failing to break a thread. We do not know whether the trackers sometimes failed to record breaks in the threads, or whether the hippopotami were going through pre-existing breaks. However, after making allowance for this error which is 13% for down-going hippopotami, it is clear that a substantial number of bushbuck and duiker failed to break the threads. We therefore incline to the view that little extra information is gained from the thread fences, and that they are not worth the considerable trouble of installation.

Table 6. *Breaks in thread fences*

	Upward		Downward	
	Tracks	Breaks	Tracks	Breaks
Bushbuck	360	248	280	195
Bushpig	226	212	221	207
Duiker	159	71	122	67
Reedbuck	47	37	31	21
Waterbuck	16	16	16	14
Hyena	7	5	6	4
Leopard	16	10	12	8
Hippopotamus	106	100	102	87

In the estimate of the mammal population, there are three possible sources of serious error to be considered. The first is that bushpigs habitually go about in parties. Our trackers, when cross-examined, were confident that these parties were never greater than five, and that they could count parties up to this size accurately from the tracks. At first we found it difficult to believe this. However, it seemed clear that if there were in fact an appreciable number of parties containing 5, 6, 7 or 8 pigs, which were being recorded as containing only 4, then the distribution of party sizes would be misshapen, with too large a number in the 4-class. Table 7 summarizes all the observations of pig parties. It can be seen that most pigs go about in two's. Threes are only half as com-

mon as ones, and fours and fives are excessively rare. Even if half the threes ought to be fours, and half the fours ought to be fives, it would make little difference to the estimate of the total population. The next possible source of error is the quality of the work of the trackers. As mentioned before, these men were not permanent employees, but locals specially engaged for these observations. Their powers of observation were tested before they were engaged, but their consciences could not be tested so easily,

Table 7. *Size of bushpig parties*

	One	Two	Three	Four	Five
Upward-going parties	103	288	59	4	1
Downward-going parties	96	282	61	4	1

and it is relevant to inquire whether their work was in fact sufficiently careful to justify the conclusions we have drawn from it. We believe that it was, for we recognized the danger, and accordingly provided intensive supervision. No tracker could ever feel confident that we would not appear from behind the next bush, and their alertness was encouraged by the necessity of recording our tracks as well as those of the wild animals. The last possible source of error lies in our assumption that all the animals drink every night. If some drink less often, then there must be more of them than we have concluded. However, while some animals are known to be able to go 2 or 3 days without drinking, it is not known that any do so from choice, and it seems probable that the majority of animals do drink at least once a day, when they live in sight of a

Table 8. *Mammal population of Nzalagobe*

	Minimum	Mean	Maximum
Bushbuck	9	13	22
Bushpig	12	15	29
Duiker	4	6	8
Reedbuck	1	2	5
Waterbuck	0	0·5	1
Hyena	0	0·7	2
Leopard	0	1	2
Hippopotamus	0	3	5
Buffalo	0	0	0
Totals	26	41·2	74

Notes. (*a*) Since we decided to adopt 8 as the probable population of duikers, the mean probable population of host animals is 43. (*b*) In April, before regular tracking began, there were two buffaloes with a calf in the area. These evidently moved away. The regular trackers recorded one buffalo irregularly in the first weeks, later none at all.

vast lake. A Kenya Game Ranger, Major E. W. Temple-Boreham, M.C., writes in a private letter, 'I agree it would be reasonable to assume that, under the conditions described, the animals would drink once a day, i.e. every 24 hours'. There is further support for the assumption in the records of tracking individual animals presented in Fig. 2, with the reservation that the duiker perhaps do not behave quite the same as the other animals. We shall do well to adopt the maximum number of tracks observed, eight, rather than the mean, six, as representing the population of duikers. Our findings about the mammal population of Nzalagobe are given in Table 8.

ACKNOWLEDGEMENTS

We are much indebted to our colleague, Mr A. N. Smit, who, after the transfer of the junior author, assumed charge of these observations and brought them to a successful conclusion. Preliminary discussions with Mr E. F. Whiteside were helpful and stimulating. The thread fences were his invention; although we have concluded that the actual threads were not useful, the mammal census is based on the idea of a fence.

SUMMARY AND CONCLUSIONS

The tsetse population of Nzalagobe was 5000 *Glossina palpalis* and 50,000 *G. pallidipes*. The population of probable hosts was 43, of which the commonest were bushpig, 15, and bushbuck, 13. Thus every animal, on the average, supported 1,163 *G. pallidipes*. It is considered probable that *G. pallidipes* would, under the local conditions, feed every 4 days, so that each animal on the average must feed 291 *G. pallidipes* a day, or two every 5 minutes assuming steady feeding throughout a 12 hr. day. *G. pallidipes* takes up about 60 mg. of blood per feed, so that each animal loses 291×60 mg., or 17·5 g. (just over half an ounce) of blood per day to the tsetses.

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SPECIES FREQUENCIES IN RANDOM SAMPLES FROM ANIMAL POPULATIONS

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(With 3 Figures in the Text)

INTRODUCTION

Two methods of describing the relation between the numbers of individuals and the numbers of species in a random sample of an animal population have so far been suggested, a logarithmic series (Fisher, Corbet & Williams 1943; Williams 1944, 1947) and a truncated log-normal function (Preston 1948). The former was obtained from the negative binomial series by elimination of the index k and of the zero term, and was found to give a satisfactory fit to the data considered. Preston, however, produced other data for which the log series was less satisfactory, and he fitted (by eye) portions of normal or Gaussian curves after grouping logarithmically. Whilst studying the composition of samples of Collembola it was found that many of these called for species-frequency distributions of Preston's log-normal type rather than of the log-series type. Instead of applying his methods, however, a return was made to the negative binomial series (with zero term omitted) as had in fact been suggested by Fisher in the paper already mentioned.

THE MODIFIED SERIES

In sampling from a population with species densities distributed in the form:

$$df = \frac{1}{\Gamma(k)} p^{-k} m^{k-1} e^{-m/p}\, dm.$$

the negative binomial series, giving the probability with which n individuals will be observed, is obtained

$$\frac{\Gamma(k+n)}{\Gamma(k).n!} \frac{p^n}{(p+1)^{n+k}} \quad (n=0,\ 1,\ 2,\ \ldots),$$

p is a parameter proportional to sample size, and k an intrinsic property of the population. As it is clearly impossible to obtain a quantity of species represented by 0 individuals, the series is developed by putting $n=1,\ 2,\ 3,\ 4$, etc., and introducing a constant, β, to each term, so that if S is the number of species in the sample,

$$S = \beta\left[\frac{kp}{(p+1)^{k+1}} + \frac{(k+1)k}{2!}\frac{p^2}{(p+1)^{k+2}} + \frac{(k+2)(k+1)k}{3!}\frac{p^3}{(p+1)^{k+3}} + \ldots\right]$$

$$= \frac{\beta}{(p+1)^k}\left[\frac{kp}{(p+1)} + \frac{(k+1)k}{2!}\frac{p^2}{(p+1)^2} + \frac{(k+2)(k+1)k}{3!}\frac{p^3}{(p+1)^3} + \ldots\right].$$

It follows that, the sum of the series, or total number of species,

$$S = \beta[1-(p+1)^{-k}] \quad \text{and} \quad N = \beta pk,$$

N being the number of individuals. The equation for S shows that β has the very useful property of being the limit of S as the sample increases in size, i.e. as p increases, and can be regarded as an estimate of the number of species in the population, provided the total sample is a sufficiently small part of the whole for the Poisson distribution for the sampling of each individual species to remain valid. The species-richness is measured (inversely) by k, for the larger it is the smaller the proportion of relatively rare species. The constants p and k can be calculated from the moments of the distribution, although a more efficient solution would be desirable:

$$\mu_1' = pk/[1-(p+1)^{-k}], \quad \text{the arithmetic mean } N/S,$$

$$\mu_2 = NS^{-1}[(k+1)p+1] - N^2S^{-2}, \quad \text{the variance.}$$

β then follows from $N = \beta pk$.

The data were grouped into 'octaves' following Preston, after calculating the first eight terms, and beyond this, only the octave boundary terms, 16, 32, 64, 128, etc. Intermediate terms in the lower octaves were found by graphical interpolation, and in the octaves from 32 to 64 onwards, the expected frequencies were calculated by means of the following approximation, which assumes linearity:

$$\text{quantity in octave } n \text{ to } 2n = n[\tfrac{1}{2}(q_n - q_{2n}) + q_{2n}],$$

where q_n = frequency at the nth term.

EXAMPLES

The use of the series will be illustrated with data on Collembolan populations collected by Agrell (1941), and by Salt, Hollick, Raw & Brian (1948). The former was collected with Tullgren apparatus in Swedish Lappland, from several habitats of increasing altitude classified as follows:

Meadow-birch-wood, leaves	*Regio subalpina*
soil	
Heath-birch-wood, leaves	
soil	
Alpine meadows	*R. alpina fertilis*
Alpine heaths	
Alpine stony soil	*R. alpina sterilis*

Samples from such habitats were taken in several localities but principally at Abisko and Torneträsk, and all the material considered below came from these localities except one sample of heath-birch-wood soil taken at Sarek. Salt *et al.* collected material from a permanent pasture (spinney pasture) near Cambridge, England, by the flotation and hydrocarbon extraction technique.

Both sets of data are very extensive, and have in addition one merit frequently lacking in other studies of species-frequency—as far as is humanly possible they are unbiased samples from well-specified natural habitats. Collembolan populations appear to be characterized by high average numbers of individuals per species, and it is inconvenient to plot a frequency distribution of numbers of species with 1, 2, 3, ..., etc., to, for example, 1347 individuals. The method of grouping proposed by Preston (1948)—into octaves 1–2, 2–4, 4–8, 8–16, ..., etc.—has been followed here for convenience of

comparison.* This grouping produces a frequency distribution from a log-series which is at first horizontal (or more strictly declining very slightly), but later descends quite steeply to the abscissa. With the negative binomial series, on the other hand, the distribution at first rises (with an approximately linear slope proportional to k), reaches a maximum and then declines to the abscissa in the same way as the log-series. It was this rise to a maximum that Preston observed, and which caused him to try fitting portions of normal curves.

Table 1. *Statistics of the Collembolan distributions*

(N=number of individuals, S=number of species; p, k and β, constants of the negative binomial series; α, the index of diversity in the log series; the values of k are expressed to the nearest 0·005.)

Sample source		N	S	β	p	k
Spinney pasture		4,859	24	33	753·1	0·195
Meadow-birch-wood	leaves	1,744	27	78	297·7	0·075
	soil	1,832	22	84	436·2	0·050
Heath-birch-wood	leaves	2,565	25	36	349·4	0·205
	soil	6,414	35	74	918·4	0·095
	soil (Sarek)	3,454	33	49	376·4	0·185
Alpine meadows		4,189	27	Log series	α=3·86	
Alpine heaths		9,033	36	Log series	α=4·70	
Alpine stony soil		11,126	27	37	1715·7	0·175

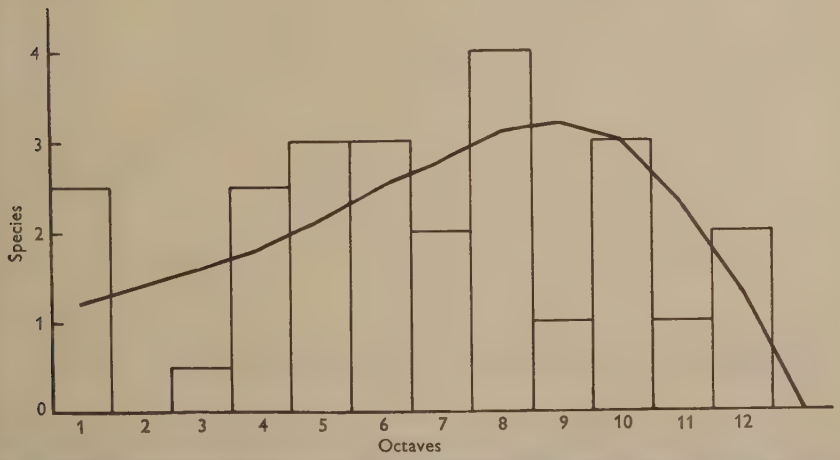

Fig. 1. Agrell's sample from Alpine stony soil: observed species-frequencies (histogram), and frequencies calculated with the negative binomial series (polygon). Abscissa: the numbers of individuals grouped into octaves, and numbered sequentially.

To seven out of the nine examples, negative binomial series have been fitted with values of k (expressed to the nearest 0·005) ranging from 0·050 to 0·205; to the remaining two, Alpine heaths and Alpine meadows, log-series. The statistics have been tabulated in Table 1 and a figure of the largest sample, Alpine stony soil, on an octave base, has been drawn (Fig. 1). The log-series was used, where, after examination of three-item moving averages, no distinct upward trend to a maximum was perceptible; the accurate but laborious test given by Fisher was not employed. Some of the samples,

* The usual method of logarithmic grouping is really preferable.

e.g. that figured, would be regarded as largely 'unveiled' by Preston, and it can be clearly seen that the distribution used differs from his in being asymmetrical (when 'veiled' regions of the normal curve are included).

Even where k is large, it has not been possible to show that the negative binomial series is significantly superior to the log-series, although in most cases the sum of squared deviations is less when the former series is employed. As an example of the degree of fitness shown, both the log-series ($\alpha = 3{\cdot}83$) and the negative binomial series for the sample from heath-birch-wood leaves ($k = 0{\cdot}205$, $S = 25$) gave, with the usual χ^2 goodness of fit test, probabilities of between 80 and 90%. In this case, the small number of species involved was probably the main factor preventing a distinction being made, in spite of the fact that the value of k was the largest observed in any of the samples. However, Miss Marjorie Thomas has had more success using the heath-

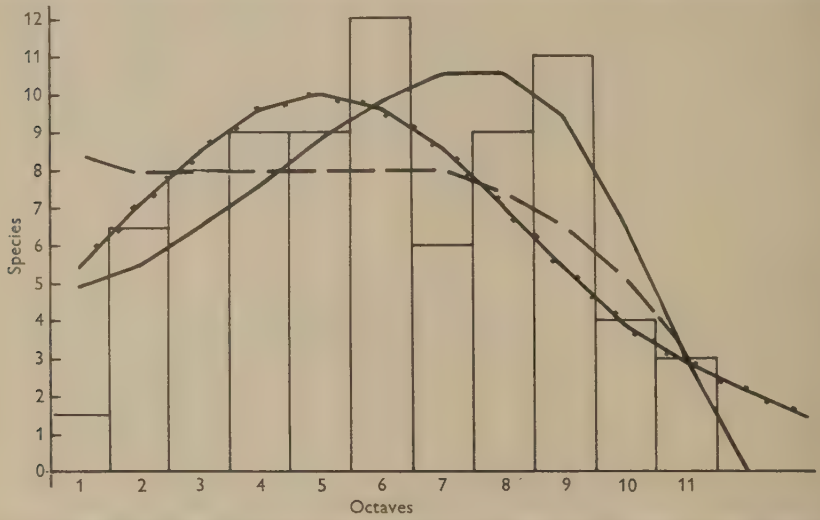

Fig. 2. Saunders's bird data: observed species-frequencies (histogram) and frequencies calculated with (*a*) the negative binomial series (continuous polygon), (*b*) Preston's truncated log-normal curve (hatched polygon), and (*c*) the log-series (broken line). Abscissa: numbers of individuals grouped into octaves.

birch-wood soil (Sarek) data ($k = 0{\cdot}186$, $S = 33$). She used the same method of calculating the parameters, and grouped the data logarithmically (but by a method which did not involve rejection of half the singletons) as follows: 1–2, 3–6, 7–14, 15–30, etc. Each of the first 126 terms were calculated (covering six groups) and the remaining frequencies, included as a single residual group, were obtained by subtraction from the total species number. Using the χ^2 test, the value 7·64 (with 4 degrees of freedom, P about 0·106) was obtained for the negative binomial series, and the value 14·77 (with 5 degrees of freedom, P about 0·011) for the log-series.

This has also been possible with the first and most striking example given by Preston, that of the bird fauna of Quaker Run Valley in New York State studied by Saunders (1936). With this set of data, log-series ($\alpha = 11{\cdot}18$) and negative binomial series ($k = 0{\cdot}200$, $p = 642$) have been developed and compared with the log-normal curve given by Preston (Fig. 2). The order of success in fitting the observed data is: negative

binomial (P about 0·321), log-normal (P about 0·232) and log-series (P about 0·099). If the deviations of the observed values from those calculated using the negative binomial series are used to measure error in the usual way, the improvement in fit of the series compared with the log-series is significant (F test: P 0·01–0·05), but this cannot be said of the log-normal curve. A critical comparison of this with the negative binomial series must await the development of better methods of estimating the parameters and of calculating the frequencies of both these distributions.

SAMPLE SIZE

Preston maintained that the Poisson correction for the effects of the sampling process could be neglected, and that as sampling proceeded the Gaussian curve (octave grouping) was drawn out from the ordinate or 'veil line', advancing an octave each time the sample size was doubled. The progress of sampling with the negative binomial distribution bears a crude resemblance to this process of unveiling. To illustrate this, Agrell's data for heath-birch-wood soil at Sarek have been plotted (Fig. 3) for two

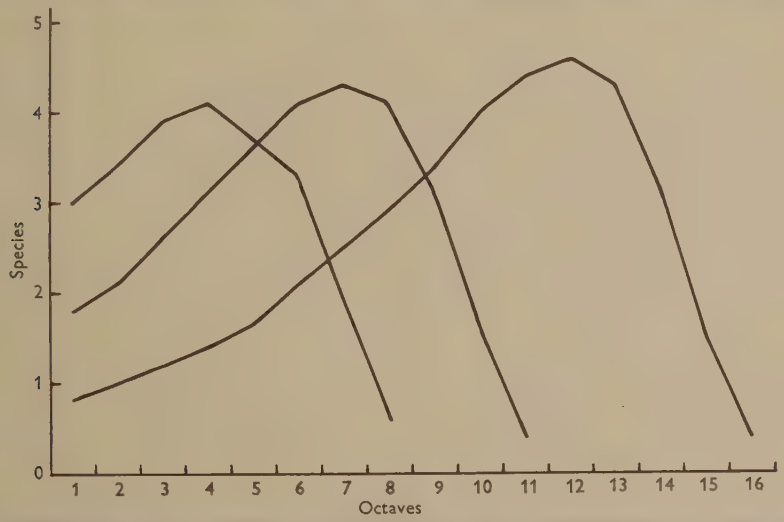

Fig. 3. The negative binomial distribution applied to Agrell's data from heath-birch-wood soil at Sarek. Three stages in sampling are shown: (*a*) 500 individuals collected (hypothetical), (*b*) 3454 individuals collected (actual), and (*c*) 100,000 individuals collected (hypothetical). Abscissa: numbers of individuals grouped into octaves.

imaginary stages, one less than the observed ($N = 500$), and one beyond ($N = 100{,}000$). Here p is 50 and 10,000 respectively. The values of S were as follows: 25, 33 (the real sample) and 36, showing between the last two stages very little increase in knowledge of species composition for an exceedingly large increase in labour. The distribution shows a progressive increase in skewness, as the frequencies in the lower octaves only fall slowly, but the height of the maximum shows little change.

As the size of the sample increases, the approach of S to β retards, following the equation

$$S = \beta\left[1 - \left(\frac{N}{k\beta} + 1\right)^{-k}\right].$$

This describes a convex non-inflecting curve approaching the asymptotic value of β. Theoretically, S can never equal β, a property derived from the form of the parent (population) distribution, but in fact, the approach to β is very close for large samples, especially when k is also large. The relationship between S and N is similar for the log-series except that S is unlimited, but for the log-normal distribution used by Preston, a point of inflexion must occur at relatively small values. Archibald (1949) contended that the growth of numbers of species with sample size (in this case quadrat area not numbers of individuals) was better described in many plant communities by a logistic equation. Unfortunately, her data do not support this conclusion, for the species increase data, when plotted on arithmetic co-ordinates, give a curve which shows no sign of inflexion, and is on the contrary similar to that expected in modified negative binomial distributions, that is, convex and non-inflecting in its approach to an asymptote. This, as does the logistic, gives an S-shaped curve when numbers of individuals (or, the sample size when the numbers of individuals is difficult to ascertain) is plotted logarithmically. No doubt the mathematical error (Archibald 1949, p. 281) contributed to this misconception.

THE POPULATION SAMPLED

The parameters β, the number of species, and k, the species-richness of the biome-segment sampled will be subject to sampling errors, and it is hoped that a method of assessing these will be provided shortly. The values of β ranged from 33 for spinney pasture up to 84 for meadow-birch-wood soil. Apart from this English pasture, two habitats had β less than 40, Alpine stony soil and heath-birch-wood leaves, and as these together with the pasture might be considered relatively simple and homogeneous habitats, the result is not surprising. Meadow-birch-wood leaves with $\beta = 74$ is less than the soil from the same locality, but the difference is not as great (and it is doubtful if it would be significantly different statistically) as the difference between the soil and leaves in the lower woodland type. The difference between the soils from the same habitats at the Abisko and Sarek localities is interesting. Finally, it is curious that the two cases where k is negligible in the Lappland data, should be associated and ecologically transitional between the sterile alpine zone and the subalpine zone. Perhaps the rare species of both habitat-types combine to produce this effect. In the log-series, $N = \alpha p$, and since in the negative binomial series $N = \beta p k$, it follows that for small values of k, $\beta k = \alpha$ approximately. Where k has the value 0·2, $\beta k = 2\alpha$ approximately; thus in the data on birds collected by Saunders and discussed by Preston $\beta k = 22{\cdot}4$ and $\alpha = 11{\cdot}2$.

The values of k, ranging up to 0·205, were clearly inversely correlated with those of β, for when k is small there are a greater proportion of rare species in the population which are correspondingly difficult to attain in sampling. The sample from spinney pasture accounted for 73% of the estimated numbers of species in the pasture, a really remarkable result when it is considered that less than a cubic foot of soil was removed from a pasture of about eight acres in area. This suggests strongly that the pattern-size of the ecosystem was very little bigger than the sample size.

For Saunders's bird data, β has the value 112, which may be compared with the equivalent estimate of 91 made by Preston. Saunders made a complete census (or

.early so) of the birds in Quaker Run Valley in Alleghany Park in New York State. He vould agree that Preston's value of 91 is more appropriate as an estimate of the total ›reeding population in the valley (the rise from the figure 80 in the census to the igure 91 could be conceived, as Preston pointed out, as being due to the 11 species of rregular breeders not present in the census year). But the census of valley birds could, ınd perhaps should, be regarded as a sample from a wider area. In this connexion it s relevant to note that Saunders also states that 114 species breed in or very near to Alleghany Park, and of this, the value 112 for β is an exceedingly good estimate. Clearly the confines of the population being sampled must be given careful considera- ion. It will be recalled that the population form that generates a negative binomial listribution when sampled is Eulerian (Fisher *et al.* 1943). For comparing curves with lifferent values of k, it is convenient to make $p=1$. Then the number of species (y) of lensity m is given by,

$$y=\frac{\beta}{\Gamma(k)}e^{-m}m^{k-1}, \quad (k>0).$$

This, since $\int_0^\infty e^{-m}m^{k-1}dm=\Gamma(k)$ by definition, integrates between zero and infinity to β, the total number of species. When $k>1$, the curve rises from zero at $m=0$ to a maximum at $m=k-1$. When $k=1$, the curve is negatively exponential with a value β at $m=0$; and when $k<1$, the curve descends continually from infinity at $m=0$. The population that Preston envisaged would be similar to the Eulerian with $k>1$, and have more medium-frequent species than rare ones. But in fact, so far (and this would include all the data given in Preston's paper) values of k so large have not been needed, and the evidence that rare species are exceedingly numerous is consequently unequivocal. The 'humping' of the octave-based frequency distribution must not be taken to suggest, as Preston supposed, that there are fewer rare species than medium-frequent ones.

As has already been implied, it is essential that samples be drawn randomly from specified ecosystems, and in such a way that the practical difficulties of deciding what are the limits of the area sampled are reduced. This was achieved in the Collembolan samplings both of Agrell and Salt *et al.*, and the former work suggested, in addition, that with transitional biomes the combination of rarer species from either extreme may be the cause of negligible values of k, and theoretically unlimited S. Conversely, it could be speculated that large values of k might be found to characterize relatively isolated or pure communities, in which case, under these conditions the type of population species-frequency envisaged by Preston would be realized.

Finally, lest the J shape of the population form suggest to the ecologist intense interspecific competition, a few well-adapted species driving a host of weaker forms into the inhospitable depths and crevices of the ecosystem to form a rich store of reserve species available in the event of a change to their advantage, it is well to recall that Kendal (1948) has shown that theoretically negative binomial distributions can develop where no competition or interference either between or within species occurs. Thus empty habitats, colonized by populations reproducing by binary fission with constant birth- and death-rates per head and constant immigration-rates, gave distributions with an index k/β = the ratio of immigration-rate to birth-rate per head.

Where immigration was relatively unimportant or negligible, the form tended towards that of a logarithmic series. In the absence of constraint as they were, these populations tended to grow geometrically at an exponential rate, with index of natural rate of increase equal to k/β (except when $\beta = \mu$ when growth depended on the immigration-rate).

ACKNOWLEDGEMENT

I am indebted to Prof. E. S. Pearson and to Dr George Salt for much helpful criticism.

SUMMARY

1. The logarithmic series is sometimes inadequate as a description of species-frequency in samples from natural populations.

2. In these cases, the use of the more general, less simplified, negative binomial series, adjusted for the removal of the zero term, should be considered as an alternative to the truncated log-normal function proposed by Preston.

3. These two differ fundamentally in the form of population assumed. Whereas the latter supposes that rare species are few, the former, although allowing for this eventuality, has so far only been found to exist in the form where rare species are the most numerous.

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NOTES ON METHODS FOR THE EXTRACTION OF SMALL SOIL ARTHROPODS

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(With Plate 1 and 3 Figures in the Text)

INTRODUCTION

Although methods for the extraction of soil animals vary much in detail they all owe their origin in principle to methods of hand sorting or to two devices developed by Berlese; the 'Berlese funnel' was invented by him in about 1895 (Berlese 1905), and so, also, was a simple flotation device described by Balogh (1948). Neither method was originally intended to extract all the animals with full quantitative efficiency, and it is in attempting to make them do this that the many subsequent variations in technique have been developed. To-day the two fundamentally distinct types of method remain, each with its devotees and its critics, and we still have no statistically valid published data on the relative efficiencies of the different methods. One conclusion, which is inescapable from the published work, is that there is no universal extraction method which can be used for all soils and all groups of animals, and therefore methods must be adapted to the particular conditions of any particular study. The following notes include some approximate comparisons of methods which are published now in the hope that they will save other workers from repeating unnecessary preliminary work. As far as possible definite problems which still need clarification are stressed, but it should be emphasized that these notes refer specifically to micro-arthropods, mites and Collembola in a size-range from about 0·1 to 5·0 mm. length. It is hoped to publish later further notes on the extraction of larger arthropods.

FLOTATION METHODS

These have been developed by Ladell (1936), and by Salt & Hollick (1944) and by Strickland (1945); they were initially developed for the sampling of wire-worm (Elateridae) larvae and other insects. However, Salt & Hollick and others have since analysed their micro-arthropod catch from the same method and come to the conclusion that this method extracts at least as high a proportion of the micro-arthropods as funnel methods do.* It would be easier to compare their method with others if some sort of comparable data were available. Unfortunately, as these authors state, the material in question was obtained on a very limited number of occasions from rather few samples, and these were taken to the unusually great depth of 12 in. (subdivided, however, into two 6 in. sections). The meadow in question has never been sampled by

* Salt (1952) has quoted general text-books as authority for estimates of soil populations which are about one-tenth those obtained with the flotation method. It should, perhaps, be pointed out that these figures are quite out of date.

other methods and no simultaneous extraction by funnel techniques was made. Perhaps the most suitable material for comparison is that of Ford (1935) which, however, was limited to Collembola and to a depth of 6 in. This came from a meadow near Oxford, and his mean figure for Collembola was 244×10^6 per acre, while Salt & Hollick found 248×10^6 per acre as a maximum. As will be shown below, Ford's figures were almost certainly low owing to his apparatus being less efficient than more recent Tullgren funnels.

Table 1. *Comparison of extraction techniques*

(Parallel trials with sixty samples divided between two treatments and three vegetation types: means per sample.)

	Flotation method			Funnel method		
	Molinia	*Deschampsia*	*Juncus*	*Molinia*	*Deschampsia*	*Juncus*
TYPICAL COLLEMBOLA AND MITES						
Total Collembola	3·0	2·0	0·3	28·9	11·1	4·9
Scheloribates	8·8	5·2	1·0	21·6	6·3	2·2
Minuthozetes	12·8	5·9	0·2	22·1	9·2	3·2
Ceratozetes	—	6·8	—	6·7	12·5	—
Nanhermannia, adult	0·4	0·9	0·1	4·1	3·8	0·7
Nanhermannia, immature	0·6	0·3	0·2	13·6	4·3	1·2
Malaconothrus	—	—	—	5·4	1·3	0·1
Hypocthoniella	1·6	0·3	—	8·1	0·4	—
Oppia sp.	8·0	4·8	0·6	21·7	8·1	1·9
Parasitids	2·0	1·7	0·4	4·2	2·4	0·6
Eupodidae	0·6	—	—	2·9	0·6	0·8
OTHER GROUPS						
Woodlice	0·4	0·2	0·4	0·4	0·4	0·4
Myriapods	1·2	0·7	0·1	1·0	0·1	0·3
Annelids	0·6	0·1	—	0·1	0·2	—
Thrips	0·2	0·7	—	0·4	—	—
Beetles, adult	0·4	—	—	0·3	0·2	—
Beetles, larvae	0·2	0·2	0·1	0·3	0·5	0·1
Dipteran larvae	—	0·3	—	1·5	1·0	0·6
EXCEPTIONAL GROUPS AND SPECIES (showing greatest numbers in flotation)						
Notaspis	0·4	0·6	0·6	1·7	0·4	0·3
Oribatella	0·6	1·7	0·1	0·1	0·1	0·3
Dinychus	0·4	0·9	0·4	0·3	0·1	0·1
Aphids	0·6	31·4	0·1	7·4	0·1	—
Totals of all animals	58·2	71·9*	7·1	174·0	72·0*	25·6

* Due to aphids.

Some direct comparisons were tried by the present author between flotation and funnel methods, but the discrepancies in favour of the latter were so considerable that it is felt that the flotation technique as used by him must involve very considerable errors. The nature of these is discussed below. A modified Salt & Hollick apparatus was used, the only differences from the published account being that the apparatus was scaled down so that all vessels were half the original capacity, and a very fine phosphor-bronze gauze of 360 meshes to the inch (say 0·06 mm. square or having holes about 0·05 mm. square) was used in place of the 0·1 mm. diameter holes used by Salt & Hollick, and considered by them to be too coarse for efficient retention of the animals. The results of a set of comparative trials are given in Table 1 which is based on sixty

amples of 50 ml., each taken from five sampling points and three plant types in a fen t Cothill near Oxford. A description of the area and fauna are given in a previous paper (Macfadyen 1952). The flotation method appears to be as efficient as the funnel method for larger insects and more so for aphids, but less so for the mites and Collembola which concern us here. An alternative method for aphids, which are evidently extracted very imperfectly by the Tullgren funnel, will be discussed below in connexion with chemical repellents.

A number of reasons can be suggested for the low yields of arthropods obtained from the flotation technique, some of which are peculiar to this experiment and others liable to apply generally to the method. The main causes of loss of animals seem likely to be two, namely, rough handling and the difficulties of separating the small arthropods from other floating matter, especially plants. The last is believed by the author to be the most serious inherent disadvantage of the flotation technique, which becomes especially serious with small hairy mites and is not completely overcome by the tedious and unpleasant benzene-water interface technique. In any investigation where time, labour or skill are at a premium, this technique is at a considerable disadvantage, and it seems unlikely that a sample could be sorted by the flotation method in less than ten times the time demanded by the Tullgren funnel method. Salt gives 3·3 days as the normal time required to sort a sample by his technique, but this does not include detailed identification of the animals.

FUNNEL METHODS

So many variations of the original Berlese funnel exist that it would not be profitable to enumerate them all here. The workers that have chiefly influenced the present author are: first Berlese (1905) applied heat to animals in soil or litter suspended in a tray over a funnel. Secondly, Tullgren (1918) first used an electric bulb suspended above the tray so as to add the stimulus of light to that of heat, and to heat the material from above and thus drive the animals downwards into the funnel. Thirdly, Ford (1937), by mounting a battery of small Tullgren funnels together, was able to treat a large number of small samples and to obtain statistically valid estimates of the populations of the several species present in the material. Fourthly, Haarløv (1947) realized the importance of condensed water, which in earlier funnels collected on the sides of the funnel itself and entrapped the weaker animals. He modified the construction of the funnel accordingly, and was the first author to attempt an analysis of the temperature and humidity distribution in the funnels during extraction. Fifthly, Hammer (1944) argued that the soil should be inverted and placed in the funnel without being disturbed and teased apart as had always previously been done, on the grounds that handling kills the more delicate animals and obstructs the passages through which they would otherwise move to the lower surface of the soil mass.

The first apparatus constructed by the present author (Fig. 1) was intended for use on expeditions and had to be portable and to use paraffin as a source of heat. It was constructed to extract thirty small (50 ml.) samples at a time with as little disturbance as possible. The apparatus was designed empirically, and no provision was made to prevent condensation on the sides of the funnels. It could, and should, be modified in accordance with Haarløv's (1947) principle, so that an air space between the steel tubes

and the funnels allows fresh air to circulate in the funnels and prevent condensation. The funnels were made of tinned iron with a slope of 40° included angle (much steeper than in previous apparatus). The use of glass funnels is very much to be preferred; experiments with plastic (celluloid) funnels have not shown these to be satisfactory. The samples are taken in stainless steel tubes 5 cm. long, $1\frac{1}{2}$ in. external diameter; the upper end of the tubes is blocked by a piece of gauze or perforated zinc (Pl. 1 *A*). The tubes are driven into the soil by means of the special holder, with the assistance of a cook's knife if necessary, and remove a core 5 cm. long and 10 sq.cm. in cross-section. The samples are inverted when placed in the apparatus so as to bring the gauze and original upper surface downwards; in this way the animals which normally live at the surface do not have to move far through the soil, while those which are able to burrow

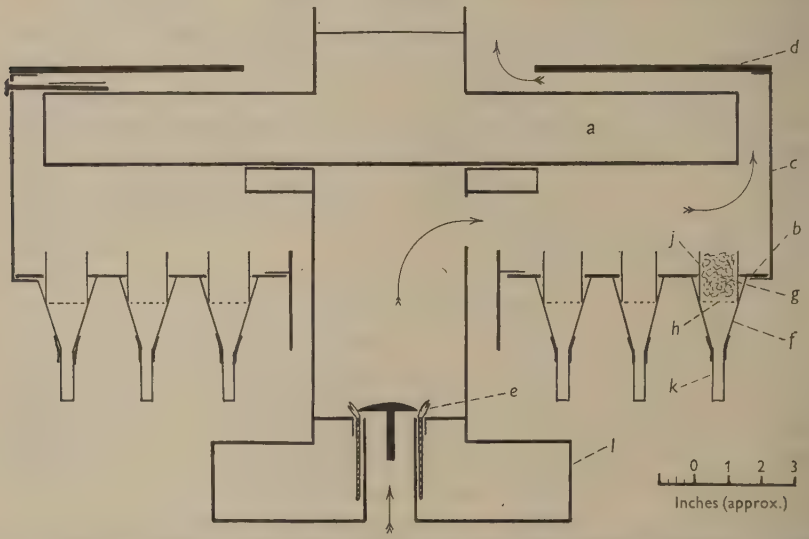

Fig. 1. Vertical section through 'Expedition' funnel-apparatus. Water-bath (*a*) stands on a paraffin-burning 'Buflam' heater and the annular disk (*b*) carrying the funnels (*f*) and the samples (*g*) is supported from it by the metal casing (*c*). Other parts labelled are: asbestos cover and baffle (*d*), flame (*e*), gauze in sampling tubes (*h*), steel tubes (*j*), $2\frac{1}{2} \times \frac{1}{2}$ in. phials (*k*), paraffin tank (*l*). The arrows show the direction of flow of the air through the apparatus.

have the greater distance to travel. The gradient of heat from above downwards, which is assisted by the metal baffle plate, produces a definite temperature and humidity gradient in the required direction instead of, as occurs in the more usual types of apparatus, a large number of subsidiary gradients towards the centres of the large crumbs of soil where one might expect the animals to become incarcerated.

For field purposes the water-bath has the distinct advantage of considerable thermal inertia which allows a fairly steady temperature to be maintained. The whole can be surrounded by sacking if fuel economy is important, and it will be seen that the air circulation is so arranged as to make maximum use of the heat which was derived from a 'Buflam' blue flame wick stove consuming about two quarts of fuel per day. The process of extraction occupied from 2 to 3 days with the very well-drained soils studied in practice, but might easily take twice as long if heavy clays were involved.

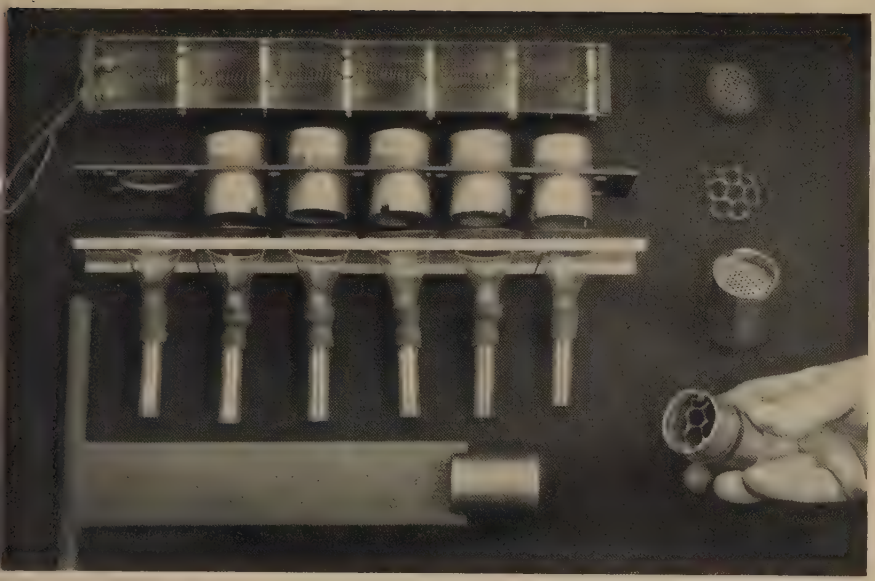

Photo: D. A. Kempson

1. Constituent parts of the 'high-gradient' funnel apparatus. The stainless-steel tubes and holder are the same as those used in the 'Expedition' type apparatus.

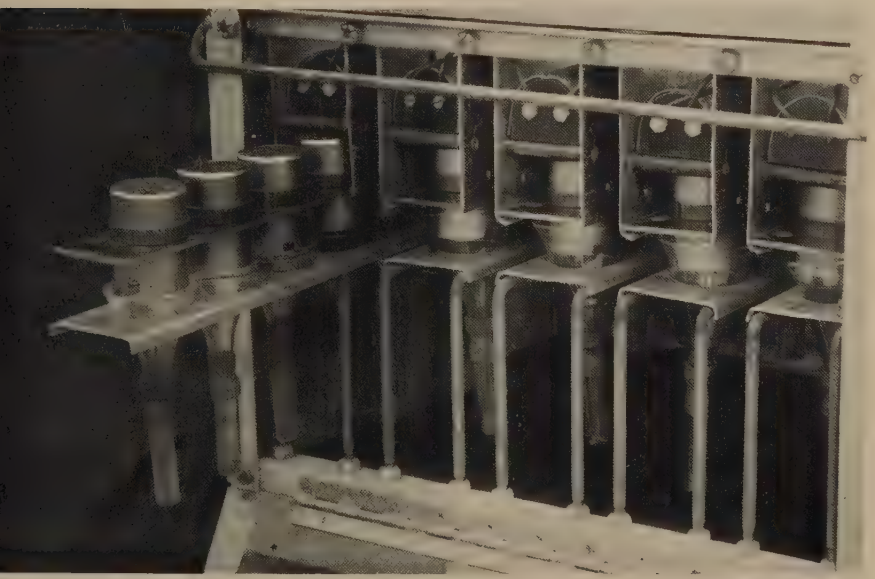

Photo: D. A. Kempson

3. The front of the 'high-gradient' funnel apparatus showing the rack method of construction and one set of samples and funnels partly withdrawn.

For normal laboratory use a further apparatus has been developed using electric eating and a more convenient system of racks to hold samples and funnnels (Pl. 1 *A*, *B*). his apparatus is termed in what follows the 'high-gradient' funnel. The same steel mplers are used and the following refinements are incorporated:

(*a*) There is a considerable gap ($\frac{1}{4}$ in.) between the funnels and the cores to prevent ondensation in the former.

(*b*) Glass funnels are used with an included angle of not more than 60° (not 90° as most filter funnels).

(*c*) By using a plastic insulating baffle plate a steeper temperature gradient is btained in each individual sample. This is about 11° C. in 5 cm.

(*d*) The temperature gradient is also assisted by making the whole apparatus on the rinciple of a chimney so that a positive flow of cold air enters from below, cooling the wer extremities of the cores, while the upper surfaces are heated by radiation from he electric coils.

(*e*) By the use of hemicylindrical aluminium reflectors the power required can be educed to about 4 W. per sample.

(*f*) There are five banks of six funnels each, each bank being controlled separately o permit experiments on the optimum rate of extraction. The banks take 12 V. each o that a 12 V. accumulator can be used as an emergency power supply demanding 10 A. or the whole apparatus. The entire apparatus is constructed on a system of inter-hangeable racks, the funnels and samples being carried in circular holes. The sample orers are held in place with springy brass clips.

The construction should be clear from Pl. 1. The time of extraction varies with the oisture content and nature of the soil but 8 days is usually sufficient. If more rapid xtraction is desired this period can be reduced to about 2 days by only half-filling the orers. The glass tubes are half-filled with 80% alcohol and the funnels are washed own with alcohol after extraction because enchytraeid and other worms sometimes dhere to the sides and may hinder the collection of other animals. This may well be source of inaccuracy but it has not been followed up.

PHYSICAL MEASUREMENTS IN THE FUNNEL APPARATUS

he design of the funnels described above was accompanied by numerous measure-ents of temperature and humidity in various types of funnel, and it was in this way at the 'high-gradient' characteristics of the laboratory version were established. hile it would not be profitable to quote many figures on the subject certain features e worth listing; some supporting data are given in Fig. 2.

(*a*) *Temperature*

Temperatures were measured by means of thermocouples and a galvanometer; the radient is normally rather steep at the upper surface and falls off roughly exponentially. he temperature throughout the soil plug is remarkably dependent on the room mperature. This is especially marked in the apparatus designed by Ford, which was ken as typical of most Tullgren funnels. Throughout these tests the Ford apparatus as loaded with samples in steel tubes (not loose soil) and differences are therefore

much reduced. Typical figures at two room temperatures for the upper and lower surfaces of the soil were:

Room (° C.)	Lower surface (° C.)	Upper surface (° C.)
19	24	27·5
24	28	31

The temperature just within the soil at the base of the sample is considerably above that of the room. This effect is less marked in the high-gradient type of funnel, while in less efficient types much of the difference in temperature between the upper surface of the soil and the room temperature occurs here. Therefore, when operating such funnels one must choose between accepting a small temperature difference between the upper and lower surfaces and, alternatively, having the whole sample, particularly the upper part, at a very high temperature. Thus in typical examples with a room temperature of 20° C. the high-gradient funnel can be operated to give a gradient of 8° C. by heating the upper surface to 36° C. (difference between base of sample and air 8° C.). In Ford's type of funnel either the same gradient can be obtained by heating the surface to 46° C., or if the surface temperature is limited to 36° C. a gradient of only 5° C. is achieved, because the difference between the lower surface and the room is 11° C. These figures are expanded in Table 2 and illustrated by histograms in

Table 2. *Temperatures in soil cores measured by means of thermocouples in different funnel apparatus*

	'High-gradient' funnel (° C.)	Tullgren funnel	
		Same gradient (° C.)	Limited maximum (° C.)
Upper surface	36	46	36
Lower surface	28	38	31
Air temperature	20	20	20
Soil gradient	8	8	5
Air gradient	8	18	11

Fig. 2. The high-gradient funnels are normally operated with a 4 W. heater; the maximum upper surface temperature is then about 33° C., but this is only attained after a period of about 2 days. It is, of course, important that the temperature rise should take place slowly.

(*b*) *Relative humidity*

Some measurements have been made on earlier types of funnel to determine the relative humidity of the air spaces in the soil during the extraction process. The cobalt thiocyanate papers of Solomon (1945) were used and were inserted in slits made in the soil sample by means of a scalpel. The method obviously leaves much to be desired, but the general indications observed are unmistakable and of some interest. In Fig. 3 humidity gradients in Ford's apparatus (modified to take cores) is compared with two versions of the 'expedition' apparatus. In the electrically heated version a heater is immersed in the water-bath and heating of the samples is by radiation only, while in the paraffin-heated version there is also heating by hot air. It is evident that:

(i) The desiccation of the air in the soil pores of the sample does not commence for some time after the extraction has started; this is due to the free water in the sample which must be evaporated before the air in the pores begins to dry.

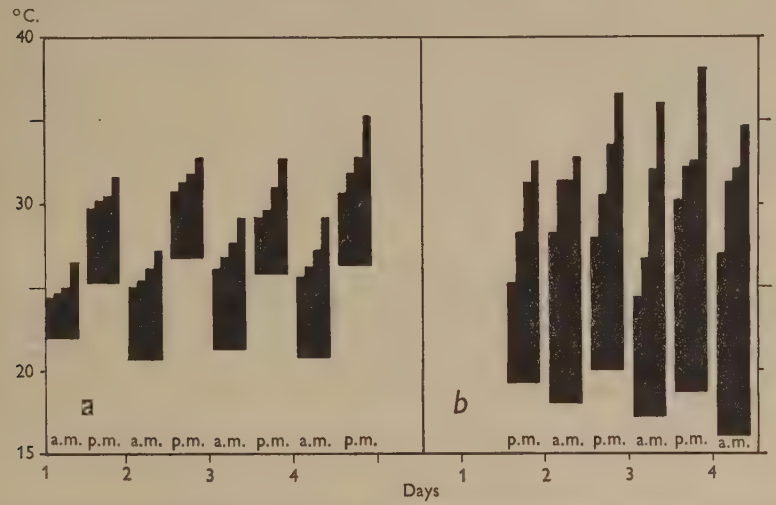

Fig. 2. A comparison of temperatures measured with thermocouples in soil cores placed in (*a*) Ford's Tullgren funnels and (*b*) in the 'high-gradient' funnels. The base of each histogram represents the room temperature, the first step in each group is the temperature at the base of the soil core, and successive steps are temperatures at two-thirds, one-third and the surface respectively.

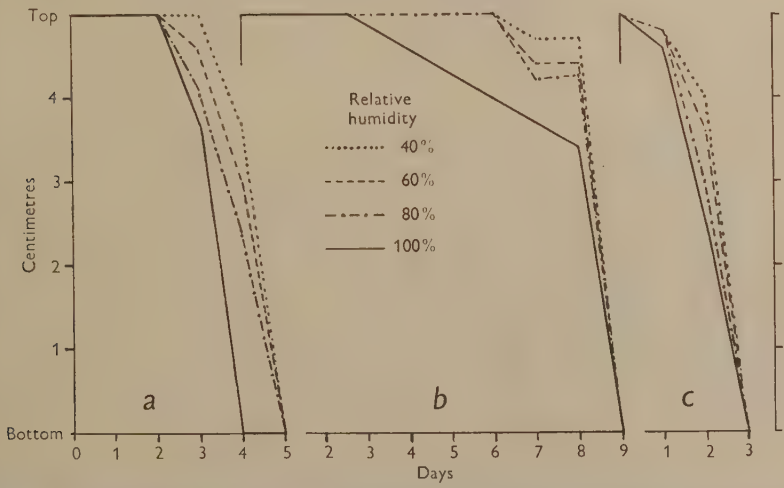

Fig. 3. 'Humidity contours' measured with Solomon's cobalt thiocyanate papers in soil cores placed in three types of extraction apparatus: (*a*) 'Expedition' funnels with electrically heated water-bath; (*b*) Ford's Tullgren funnels; (*c*) 'Expedition' funnels with paraffin-heated water-bath.

(ii) When desiccation of the air starts at any one level in the sample, it proceeds rapidly, taking a small proportion of the extracting time; this must be important for the air-living organisms with which we are here concerned.

(iii) There is a tendency for the humidity changes to move from the surface downwards; this should result in the animals being driven downwards towards the funnel.

Haarløv (1947) showed a similar sudden drop in humidity using the Nielsen and Thamdrup (1939) sulphuric acid method of humidity determination in his own type of Tullgren funnel, in which the soil is teased apart. He showed that the drop in humidity coincides with the exodus of certain species which appear to be resistant to the elevated temperature alone. Although no similar correlation was established in the present study, Haarløv's results have been confirmed for larger funnels and must almost certainly apply in the 'high-gradient' funnels also.

EFFICIENCY OF DIFFERENT TYPES OF FUNNEL

Comparative estimates (Table 3) of the efficiency of different funnels have been made for the 'high-gradient' type, Ford's multiple Tullgren type, the paraffin-heated 'Expedition' type, and also a funnel in which repellent chemicals were used instead of heat to drive the animals down through the soil. These last used 'gammexane'

Table 3. *Mean total populations extracted from thirty samples, each of 10 sq.cm. by various methods*

(The samples were taken in *Molinia coerulea* fen at Cothill (Near Oxford). All figures except those linked by brackets are significantly different ($P < 0{\cdot}05$).)

Type of funnel	Collembola	Mites
'High-gradient'	13·6	62
Ford's Tullgren	5·8	40
Gammexane	6·2	13
DMP	4·8	13
'Expedition'	3·0	22

(benzene hexachloride), DMP (dimethyl phthalate) and DNOCHP (dinitro-*ortho-cyclo*-hexyl-phenol), and were certainly less efficient than heat funnels for most mites and Collembola, although they were distinctly promising for aphids and for thrips.

A serious source of loss of animals was not suspected at the time these tests were made. The results in Table 4 were obtained with material from another locality with a rather sticky soil and the only difference in treatment between the two sets of fifteen samples is that while one set was treated directly in the 'high-gradient' funnels, each sample of the other set was first pushed out of the steel borer by means of a piece of wood, was bisected to produce two cores of 2·5 cm. depth and each of these was then replaced in a steel borer before extraction. Many workers have used cylindrical borers with a piston for ejecting the samples, and it is therefore of some importance to find that this handling treatment had the effect of reducing the extracted mite population by about 71% and the Collembola population by about 80%. While these results may exaggerate the source of error somewhat, there can be little doubt that handling constitutes an important source of loss in many funnel techniques.

The absolute efficiency of an extraction process is extremely difficult to establish, and almost certainly varies from species to species and from one soil type to another. One type of check which is frequently suggested involves placing known numbers of

animals in an inert medium such as sawdust or sand and then applying the technique to this 'sample'. A better alternative would be to use natural soil and either sterilize it in some way before inserting the animals or else to use marked animals. In practice, however, such tests are extremely difficult to carry out, partly owing to the errors introduced by manipulation (see above), and partly because the greater part of the fauna inhabits the layers of soil near the surface. If the experimental animals are placed at the surface they do not have far to go and all pass into the funnel, probably without the stimulus of the heat. If they are placed deep in the soil many do not come out, but this may be due to faulty handling or to inserting them in places where no suitable passages exist or to the inability of the animals to burrow through the soil because they normally live nearer the surface.

Table 4. *Comparison of two sets of fifteen samples from* Brachypodium *grassland, to show the effect of handling on the number of arthropods extracted from soil samples by 'high-gradient' funnels (numbers per sample)*

	Divided sample	Undivided sample	Ratio
COLLEMBOLA			
Tullbergia spp.	0·20	0·93	4·56
Friesea mirabilis	0	0·40	—
Neelus minutus	0·53	2·67	5·04
Others	0·47	2·14	4·55
Total Collembola	1·20	6·14	5·12
ORIBATEI			
Scheloribates latipes	0	0·93	—
Minuthozetes semirufus	0·67	2·54	3·82
Ceratozetes mediocris	0·07	0·73	10·04
Oppia spp.	0·34	1·33	3·91
Others	1·20	3·74	3·11
Total	2·28	9·27	4·06
PARASITIFORMES	0·33	1·20	3·60
TROMBIDIFORMES	1·67	4·47	2·68
Total Mites	4·28	14·94	3·49

Forsslund (1948) published the results of experiments, in which he compared the numbers of animals extracted by a Tullgren funnel from samples of two sizes with those obtained by careful direct counting of adjacent small samples. Van der Drift (1951) has discussed Forsslund's claim that the Tullgren funnel is very inefficient (Table 5, last two columns), and suggested that part of the discrepancy at least is due to animals which are temporarily immobilized by moulting. This factor may vary in importance with the speed of extraction. To the present author it appears that direct counts are likely to err on the high side because it is very difficult to distinguish animals which have died recently in nature from those killed by the sorting technique. Since Forsslund's funnel appears to be a straightforward Tullgren one, as described in his 1945 paper, and in view of the various improvements which Haarløv and the present author believe to have been made to the apparatus it was of importance to attempt to repeat Forsslund's experiment using an improved funnel apparatus. For this reason a check was made using a rather greater number of samples and the 'high gradient' funnel.

Thirty tubes of 10 sq.cm. section were driven into a rectangular 'uniform' area of soil in a nettle bed in spring (before the nettles were through the ground). The tubes were adjacent to one another and arranged in five rows and six columns. In the twenty interstices between these 10 sq.cm. tubes were placed four rows and six columns of smaller tubes to the same depth but with an area of 0·79 sq.cm. The larger samples were treated in the normal way in the 'high-gradient' apparatus, while the smaller ones were immediately placed in tubes of 80% alcohol and were later sorted under a compound microscope using not less than 40× magnification.

Table 5.

(Mean numbers per 10 sq.cm. of soil.)

			Ratios: Funnel method/direct count		
				Forsslund (1948)	
	Direct count	High-gradient funnel	High-gradient	24 c.c.	100 c.c.
THICK-SKINNED ORIBATEI					
Minuthozetes	4·45	5·13	1·15	—	—
Scheloribates	5·08	4·90	0·97	—	—
Tectocepheus	2·54	2·47	0·97	—	—
Notaspis	1·27	1·67	0·76	—	—
Pelops	4·45	3·03	0·68*	—	—
Others	4·45	0·37	0·08**	—	—
Total	22·24	17·57	0·79	0·62	0·55
THIN-SKINNED ORIBATEI					
Oppia	5·08	1·53	0·30**	—	—
Oribatei nymphs	6·35	1·87	0·29**	—	—
Total	11·43	3·40	0·30**	0·27	0·16
PARASITIFORMES	10·8	2·37	0·22**	0·49	0·52
TROMBIDIFORMES	10·8	5·17	0·48**	0·51	0·31
COLLEMBOLA					
Tullbergia	3·2	0·43	0·13**	—	—
Others	12·7	5·00	0·39**	—	—
Total	15·9	5·43	0·34**	0·27	0·24

* significant ** highly significant

It was apparent from a few exploratory trials that this hand-sorting technique would be very time-consuming and that it would, for instance, be virtually impossible to perform accurately in a clay or highly organic soil; it was for this reason that a sandy soil was chosen. Furthermore, an alcohol flotation device employing a rapid stream of alcohol and 60μ mesh copper gauze was used to remove the larger sand grains from the samples. This was thoroughly tested and shown to remove no animals with the sand grains, but despite its use a rate of sorting much in excess of 1 c.c. of soil per day was not achieved. The rectangular layout was originally used so that the more sensitive analysis of variance technique could be used to discriminate between the techniques. However, the results were so clear-cut, that in Table 5 significance as assessed by a simple T test is quoted. The table shows the analysis by species of the two counts, the figures for direct counting being multiplied by 12·7 so that all figures represent numbers per 10 sq.cm. area. The fourth column shows the ratios of these figures, and the last two columns are Forsslund's results for comparison.

In most respects Forsslund's results are strikingly confirmed. Two reservations should, of course, be borne in mind when comparing such figures. First, the soils in question were extremely different, Forsslund's being a highly organic one, and the techniques might be expected to vary in efficiency with different species and soil types. Secondly, it is not certain that the hand-sorting gives a true estimate of the actual population for the reasons given above. Despite these reservations, it seems reasonable to conclude that the 'new estimates for Parasitiformes are very low, those for thick-skinned Oribatids are higher than Forsslund's and those for other groups are much the same. Thus the apparent improvements in technique brought about by the elimination of condensation, the use of undisturbed cores and the application of the high gradient principle seem to have been confined in their effect to the thick-skinned Oribatei. (The error in the count for 'others' is very large, and the figure of 79% for total efficiency is almost certainly minimal, while the difference between the two estimates for *Pelops* is only just significant.) The low figure for Parasitiformes was something of a surprise but, on reflection, is believed to be due to escape of these larger, more active mites from the apparatus. Forsslund's type of funnel, with no air gap, would certainly be much less easy to escape from; also there is a much larger proportion of the very active *Gamasina* in the nettle bed locality than in Forsslund's raw humus soils. Fortunately this mainly carnivorous and usually less common group of mites is not of importance in the author's own studies (Macfadyen 1952) on the herbivorous and fungivorous elements of the soil fauna, but it points to a serious weakness of the apparatus which may well account for some of the losses of Trombidiformes and Collembola which are also very active.

DISCUSSION

Evidently an extraction apparatus designed in the light of these results should embody a number of new features:

(1) Despite the low figures for some groups obtained by repeating Forsslund's experiment, the greater efficiency of the anti-condensation and high-gradient principles is held to have been demonstrated and these should be incorporated.

(2) It is unlikely that any one apparatus will be 100% efficient for all groups and, in view of the vastly different densities of different groups, it is likely to be most profitable to take several series of samples and extract each by appropriate methods for each taxonomic group in turn. If an ecological problem can be confined to a single group much labour will be saved.

(3) As pointed out by botanical and statistical authors (Neyman 1939; Barnes & Stanbury 1951; Thomas 1949; Goodall 1952), but so far ignored by students of animal ecology, the basic assumption of most comparisons of density, that the organisms are distributed at random, is manifestly untrue in most cases. These authors advocate fitting of sample data to a double Poisson series, and the calculation of two parameters representing respectively the number of patches per unit area and the number of organisms per patch, on the assumption that these two are distributed at random. This not only has a much surer theoretical foundation but also has been shown to work in practice for a number of plant communities. It is certainly desirable, therefore, to try this method of analysis in the field of animal soil populations. When such methods are

used the most economical sampling technique is to employ small samples so that the species in which one is mainly interested will be absent from a fairly high proportion of samples. The dominant species of mites occur in densities from 1 to 10 sq.cm. and most important species have densities in excess of 0·1/sq.cm. In order that the above conditions can be satisfied, therefore, samples of the order of 1 or 2 sq.cm. area should be used in large numbers rather than the relatively large samples generally used hitherto.

(4) Much ecological work can be concentrated on a few commoner species, and the ecologist working on productivity studies, for instance, must resist the temptation to waste energy on the rarities, despite their taxonomic interest; the use of smaller samples becomes practicable when this principle can be adhered to, because the size and number of samples can be reduced for a given degree of accuracy.

(5) The probability that the more active forms escape from the high-gradient funnel as it stands and the need to avoid the trapping of animals on the sides of the funnels, which is especially liable to happen where worms and Enchytraeidae are present, points to a new design of apparatus in which the true funnel is eliminated altogether. The use of vertical-sided tubes becomes practicable when small samples are used and should satisfy both these requirements.

In fact, when any new soil ecological study is planned, pilot experiments on efficiency of techniques and the normal densities of the organisms, not forgetting a tenfold annual variation in density (see Macfadyen 1952), are essential. It is on the above lines therefore, and bearing in mind the need for a thorough investigation of all available techniques both automatic and mechanical, that the development of accurate soil sampling methods must lie.

ACKNOWLEDGEMENTS

I am greatly indebted to Mr D. A. Kempson who discussed many of the practical problems of construction with me, made part of the high-gradient apparatus and took the photographs. For the generosity of Tube Products Ltd., who provided without charge the stainless steel tubes used for taking the soil samples, I wish to record my grateful thanks.

SUMMARY

1. Two developments of the Tullgren-type funnel for the extraction of soil organisms are described; the first is a paraffin-burning model for expedition conditions, the second an electrically operated type for laboratory use.

2. The efficiency of these devices is compared with that of other funnels and with a flotation technique and with hand sorting.

3. A number of faults in the methods are exposed and suggestions for a more efficient apparatus are discussed; it is probable that the present technique is nearly 100% efficient for the thick-skinned Oribatid mites. The need to adapt techniques to different soil types and taxonomic groups is emphasized.

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A MIXED POPULATION OF *GLOSSINA MORSITANS* AND *G. SWYNNERTONI*

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(With 1 Figure in the Text)

METHODS

By the use of nine different colours, used two at a time, it is possible to mark upwards of 25,000 tsetse-flies (*Glossina*) without duplication, thus avoiding the need for re-marking on recapture.

The thorax of *Glossina* is divided by a transverse suture with a central pale spot (Fig. 1), and there is also a posterior suture behind which is the scutellum. Ten positions are recognized on the periphery of the dorsum such that (*6*), (*7*), (*8*) and (*9*) on the left side correspond to (*4*), (*3*), (*2*) and (*1*) on the right, (*0*) and (*5*) being median. In addition, four central positions may be distinguished.

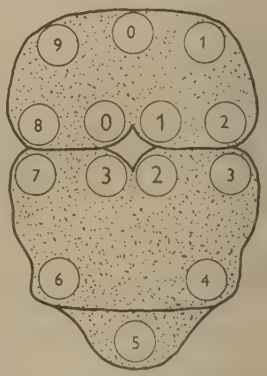

Fig. 1. Thorax of *Glossina*.

On any date, two colours are used, of which two spots of the first and one of the second are applied. The two spots of the first colour give the number of the fly in hundreds and tens and the third spot (of the second colour) gives the units. The four central positions are to indicate the hundreds and the ten peripheral positions are for the tens and units.

Thus a fly marked yellow just to the right of and in front of the centre (position *1* central), yellow behind the head in the middle line (position *0* peripheral) and white on the left side just in front of the scutellar suture (position *6* peripheral) would read *YW 106*.

As two spots cannot of course be applied in the same position, multiples of eleven are omitted within each of the four possible series of peripheral marks, together with the numbers 100, 200 and 300. This leaves 360 possible markings for each pair of colours used. With nine colours (dark blue, light blue, dark green, light green, red, pink, orange, yellow, white), which can of course be used in either order in pairs, for example, *YW* or *WY*, there are seventy-two colour combinations, allowing 72×360 or over 25,000 individual marks. The highest figure that can be applied with any pair of colours is 398.

In the field the marks are kept as small as possible, and applied with a very thin spindle of wood about 6 in. long, sharpened at both ends. They are made from artist's oil paints mixed with a little megilp, and compounded from the colours sold as deep ultramarine, vermilion, chrome-yellow mid, and flake white. Other colours have been found unsatisfactory.

It is not difficult to apply the marks correctly, and most mistakes arise from misreading them. They have been used with success by trained African fly-boys.

The amount of information that can be obtained from work of this kind may be increased by the identification of a number of catching and releasing points distributed evenly through the area studied. This may be accomplished by disposing them evenly (at say 50 or 100 yd. intervals) along the coils of an 'angular spiral'. The introduction of the fixed catching points at regular intervals was due to Mr J. Ford of this Organization, and was designed especially to bring out relations to vegetational ecotones and details of topography which are apt to be overlooked when the sectors of a fly round are laid out to correspond only to vegetational types as seen by the observer beforehand. The distance which should separate the rings is governed by local conditions and may be found by trial on the spot. For population estimations, they should be close enough to secure a random sample of the flies of the area, whether resting on the paths or half way between them.

RESULTS

The experimental block, in which the observations about to be described were made, lay north of Gedamara Hill in Tanganyika Territory at an altitude of about 1300 m. (4000 ft.) in the position lat. 4° 17′ S., long. 35° 53′ E. The marking area comprised

Table 1. *Numbers of days on which game animals of different species were seen in the block during the marking work*

	Jan.–Feb.	Mar.	Apr.	Total
Giraffe	1	—	1	2
Roan antelope	3	—	—	3
Coke's hartebeest	3	1	6	10
Greater kudu	5	3	3	11
Bohor reedbuck	—	1	1	2
Common duiker	1	2	—	3
Impala	8	12	8	28
Zebra	1	2	3	6
Total	22	21	22	65

Spoor of eland and wart-hog was also present.

a quarter of a square mile of *Acacia* and *Combretum* bushland, surrounded by a wide clearing. The path was 3800 yd. long. Two species of tsetse fly were common in this isolated block, *Glossina morsitans* Westwood and *G. swynnertoni* Austen; *G. pallidipes* Austen has been recorded once. *G. morsitans* had been the more numerous during the previous dry season (1950) but at the time of the present observations (rains of early 1951) *G. swynnertoni* was in excess. Large numbers of game—mostly impala, hartebeest, kudu and zebra, but also giraffe, roan, eland, reedbuck, duiker and wart-hog, visited the block (Table 1).

Tsetse fly populations can be estimated in either of two ways. We can find the proportions of marked to unmarked flies at regular intervals after release and so extrapolate the proportion of marked to unmarked at the moment of marking, from which the population is obviously calculable. Alternatively, we can find what proportion of the surviving marked flies was formed by flies recaptured on any one occasion, and

hence estimate the proportion of the total population caught on that date. For example, if the individual marked flies re-caught and again released on any one occasion are found in subsequent samples to form a twentieth of the recaptures of all flies marked before that date, then presumably we were seeing a twentieth of the total population on that day. Formulae for both methods will be found elsewhere (Jackson 1948, pp. 91–4). The first method is concerned with the proportion of recaptures to total catch, and the second with the proportion of re-recaptures among recaptures. An attempt was made to compare estimates made by the two methods (Jackson 1948, tables 7 and 8). The re-recapture method often tended to give somewhat higher values, but in those observations the recaptures had been re-marked, which may have unduly lowered their viability at certain seasons. In the present experiment, where flies were not re-marked, there would be no such effect. Estimates by the two methods, though not entirely independent, are very largely so; all refer only to non-teneral males. The

Table 2. *Non-teneral (NT) males at Gedamara, 1951*

	G. morsitans			*G. swynnertoni*		
	Feb.	Mar.	Apr.	Feb.	Mar.	Apr.
Population (*a*)	139	69	32	244	185	76
(*b*)	129	71	44	233	181	79
(*b*) per sq.mile	516	284	176	892	724	316
Apparent density	46	28	23	66	48	44
Availability, %	8·9	9·7	13·3	7·4	6·7	13·9
Hunger (M.H.S.)	3·11	3·24	3·14	2·86	2·89	2·75
Females, %	10·2	23·5	6·2	5·2	7·8	5·2
Teneral males, %	6·8	8·4	0·9	4·2	7·5	1·2

(*a*) = by extrapolation from recaptures.
(*b*) = by re-recaptures, without using extrapolation.
Apparent density (A.D.) is number of non-teneral (*NT*) males per 10,000 yards.
Availability % is 100 × A.D. divided by population per sq.mile.
M.H.S. = Mean hunger stage (Jackson 1933).
Females are given as % of total *NT* flies, and teneral (*T*) males as % of total males.
Three days of January are included in February.

full data and examples of working are given in the Appendix. The principal results are summarized in Table 2 from which several conclusions can be drawn. The good agreement found between the two methods of estimating the population may increase our confidence in both; it also proves that the catchers do not (as has been suggested) concentrate on catching the marked flies, whether or not because they are easier to see; for if they did, then the first estimate, from recaptures among total flies, would be lower than the second, which is found from the proportion of re-recaptures among recaptures, all of which are equally conspicuous.

For the whole period, the mean survival of *morsitans* in the block was estimated at 19 days (see Table 4) and for *swynnertoni* at 12 days; evidently the second species, at least, was escaping from the area, for which the calculated 'death' rate of course includes emigration if any. There was evidence that *swynnertoni* but not *morsitans* was escaping across the clearing. In an unconfined area, the percentage of re-recaptures tends to be higher after the second capture than after the first, and to be higher again after the fly's third capture than after its second. This is probably because flies do not inhabit equally all parts of their environment, but tend to live in ambits (Jackson 1941)

which may overlap, be contained in or lie quite outside the boundaries of the marking area. A fly already recaptured is thereby shown to be a probable resident of an ambit wholly or mainly within the marking area, and if it is again recaptured this probability is increased. When, however, the marking area is surrounded by a clearing which flies cannot cross, all the ambits must lie inside it, so that a fly already recaptured is no more likely to be recaptured again than it was before. In the present experiment the percentage of individual *morsitans* marked in February and recovered after their first, second, ..., ninth capture was (see Appendix): 59, 61, 59, 47, 64, 43, 80, 60, and 0.* These figures show no tendency to rise at the start, and indicate that *morsitans* was fairly well confined by the clearing. On the other hand, the corresponding figures for *swynnertoni* were 33, 33, 41, 62, 38, 40, 50, 0, –, showing some tendency to rise after the second capture and thus supporting the suggesion made above that *swynnertoni* was escaping across the clearing, which contained much felled and leafless but unburned timber.

About a third of the *swynnertoni* flying, and three-fifths of the *morsitans*, were marked. At first sight this might suggest higher activity (availability) of *morsitans*, but inspection of Table 2 shows only slightly higher availability for *morsitans*, and then in February and March only. The explanation may well lie in the coming and going of *swynnertoni* across the clearing, which shortens the time that marked individuals stay in the block, and brings unmarked flies to replace them. It might also be that the death-rate of *swynnertoni* is higher, but this is perhaps unlikely because, as always happens when the two species overlap, the *morsitans* males are consistently much hungrier than the *swynnertoni* (Table 2), a conclusion supported also by the higher percentages of female and teneral flies.

During the observations, populations of both species were falling at about the same rate; availability rose in April when it was wetter, hunger fell, and teneral flies and *NT* females were proportionately few. It is noteworthy that the standard availability varied from 6·7 to 13·9% for *swynnertoni* and from 8·9 to 13·3% for *morsitans*. The higher values are similar to those obtained for *morsitans* at Kakoma (Jackson 1944). It seems probable that the present figures may be rather low, because in the quarter-square-mile block some flies would see the catching party more than once in its daily traverse of 3800 yd. Generally it is obvious that the greater hunger of *morsitans* does not cause it to be much more available, and indeed, for each species separately, hungrier periods tend to be associated with lower activity, as I have observed elsewhere.

The two species showed a certain amount of segregation, *morsitans* being mainly in woodland of *Acacia spirocarpa* Hochst. and *swynnertoni* in more open bushland of *Combretum zeyheri* Sond. At this season (rains) both species avoided the thicketed parts of the *Acacia* woodland, and few were found by the thicketed stream traversing the block. Twelve pairs of copulating flies were observed, in ten of which the males were *swynnertoni* and in the remaining two they were *morsitans*. Of each species, exactly half the males had paired with females of the alternate species, and half with their own.

* In an unconfined area the corresponding respective percentages were: 22, 26, 31, 32, 26, 37, 33 0, 0, —. The first two rises are significant.

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I am indebted to Mr K. S. Hocking of the Colonial Insecticides Research for permission to use their isolated block, to Mr J. A. Gledhill for information on the position there in 1950 and for the map, and to Mr J. M. B. Harley for help in extracting the data. The fly-boys under Juma Lizani deserve special mention for careful work.

SUMMARY

1. A system of marking has been designed whereby 25,000 tsetse-flies can be marked without duplication, using two different colours at a time. This obviates the need for re-marking on recapture.

2. The information derived from such observations can be much increased if the catching points are spaced at equal intervals along an 'angular spiral' path.

3. Very satisfactory agreement was found in an isolated block of bush between estimates of *Glossina morsitans* and *G. swynnertoni* populations made respectively by extrapolating from corrected recaptures and without extrapolation from re-recaptures.

4. The agreement proves that the catchers do not tend to select the marked flies.

5. Survival of males of both species in the isolated block was short, and in the case of *G. swynnertoni* there was evidence that this was partly because flies were coming and going across the surrounding clearing, which contained much unburned trash.

6. The two species were about equally 'active', and 'activity' (availability) of both rose in April, when few tenerals and females were caught and hunger was low. *G. swynnertoni* was always less hungry than *G. morsitans*.

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APPENDIX

NUMERICAL RESULTS

Table 3. *Recaptures of non-teneral males, Gedamara, 1951, by half-weeks*

G. morsitans

January	February	March	April
29 to 31	1 5 8 12 16 19 22 26 to to to to to to to to 3 7 11 14 18 21 24 28	1 5 8 12 15 19 22 26 29 to to to to to to to to to 3 7 10 14 17 21 24 28 31	3 6 10 13 16 19 24 27 to to to to to to to to 5 8 12 15 18 23 26 29

8	3	14	6	6	7	8	3	.	3	2	1	5	6	2	3	3	6	5	1	1	4	2	5	.		
61	15	5	13	4	5	6	5	3	.	4	7	5	4	.	2	6	6	3	1	1	3	5	2	1	3	
26	18	6	2	3	9	4	6	1	.	4	4	.	4	2	1	2	2	2	.	1	5	3	.	7		
63	6	3	4	4	6	3	6	.	1	3	1	2	4	1	2	6	4	1	.	3	3	5	7			
75	3	6	5	3	6	.	1	2	2	1	2	.	2	1	1	4	6	.	1	.	1	10				
56	3	4	2	5	3	3	.	.	.	3	1	.	4	1	.	2	5	1	.	2	8					
44	3	2	4	1	.	2	3	.	.	.	1	.	1	3	.	1	7	.	.	8						
60	2	1	.	1	1	.	.	1	.	.	.	1	2	.	.	2	.	7								
57	2	3	.	.	3	.	.	.	.	.	.	.	.	1	.	.	2	.	9							
35	3	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	5								
52	.	.	.	.	.	.	.	.	2	.	.	.	.	1	.	.	12									
35	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10										
24	.	.	.	.	.	.	.	1	.	.	.	.	.	1	8											
36	.	.	.	.	.	.	1	.	.	.	.	.	15													
43	.	.	.	.	.	.	.	.	.	.	.	13														
22	.	.	.	.	.	.	.	.	.	.	9															
27	.	.	.	.	.	.	.	.	.	12																
26	.	.	.	.	.	.	.	.	20																	
19	.	.	.	.	.	.	.	4																		
33	.	.	.	.	.	.	10																			
26	.	.	.	.	.	.	24																			
27	.	.	.	.	.	18																				
24	.	.	.	.	22																					
27	.	.	.	33																						
34	.	.	38																							
23	.	16																								
14	56																									

G. swynnertoni

January	February	March	April
29 to 31	1 5 8 12 16 19 22 26 to to to to to to to to 3 7 11 14 18 21 24 28	1 5 8 12 15 19 22 26 29 to to to to to to to to to 3 7 10 14 17 21 24 28 31	3 6 10 13 16 19 24 27 to to to to to to to to 5 8 12 15 18 23 26 29

9	7	15	9	10	4	6	4	2	5	8	2	3	5	1	2	5	12	9	7	6	3	8	5	5		
66	12	4	7	1	7	9	2	4	4	4	4	4	.	3	.	3	1	3	6	6	5	2	2	2	22	
45	5	2	3	2	8	4	3	8	1	5	5	.	.	3	.	.	6	1	6	7	2	4	2	26		
91	7	2	2	1	5	1	2	2	2	4	1	1	.	2	.	.	.	4	2	4	3	29				
98	2	1	2	.	5	3	.	2	3	1	.	.	.	1	.	.	.	2	2	1	.	42				
92	1	.	1	1	1	2	.	.	.	1	.	.	1	.	.	.	.	.	3	2	34					
58	2	1	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	26						
56	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	29							
93	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	25								
63	.	.	2	.	.	.	.	.	.	.	2	.	.	.	.	.	34									
81	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	18										
83	.	.	.	.	.	.	.	.	.	.	.	.	.	.	24											
67	.	.	.	.	.	.	.	.	.	.	.	.	.	24												
54	.	.	.	.	.	.	.	.	.	.	.	.	47													
71	.	.	.	.	.	.	.	.	.	.	.	29														
32	.	.	.	.	.	.	.	.	.	.	46															
34	.	.	.	.	.	.	.	.	.	56																
25	.	.	.	.	.	.	.	.	61																	
49	.	.	.	.	.	.	.	42																		
46	.	.	.	.	.	.	59																			
55	.	.	.	.	.	34																				
42	.	.	.	.	34																					
56	.	.	.	59																						
69	.	.	67																							
48	.	65																								
49	33																									
39	64																									

The numbers initially released on the dates shown appear on the right-hand side of the tables, opposite their dates. The total numbers caught, including recaptures, appear on the left-hand side, also opposite the appropriate dates. The recaptures occupy the body of the tables, reading from upper left to lower right opposite the dates of their initial release, and from lower left to upper right opposite the dates of their recapture. Flies recaptured for the second, third, etc., time are shown on each occasion against the date of their initial release, only, and opposite the date of each recapture.

Table 4. *Corrected recaptures of non-teneral males, derived from Table 3*

G. morsitans

January	February								March								April							
29	1	5	8	12	16	19	22	26	1	5	8	12	15	19	22	26	29	2	6	10	13	16	19	24	27
to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to
31	3	7	11	14	18	21	24	28	3	7	10	14	17	21	24	28	31	5	8	12	15	18	23	26	29
	55	30	49	32	62	65	58	86	.	43	69	31	89	182	93	115	132	364	214	53	52	185	59	311	.
		43	42	61	28	38	58	60	58	.	83	162	129	140	.	96	316	152	231	41	60	139	184	87	102
			43	67	12	15	72	63	48	29	.	56	78	.	114	51	35	61	64	148	.	63	184	163	.
				19	43	18	21	78	32	71	.	69	35	38	82	118	35	40	231	123	83	.	126	163	146
					12	63	23	26	52	.	17	56	58	23	62	.	81	20	26	148	208	.	33	.	89
						9	44	15	29	39	69	.	.	.	56	32	.	93	26	.	83	154	59	.	204
							9	36	20	9	.	31	29	.	.	.	44	.	30	74	.	37	172	.	.
								10	12	.	13	13	.	.	37	.	.	.	.	28	56	.	.	72	.
									7	54	.	.	32	.	.	.	.	.	.	32	.	.	87	.
										15	26	.	.	.	.	.	.	.	.	.	.	20	.	.
											.	.	.	.	.	.	61	.	.	.	23	.	.	
												.	.	.	.	.	.	.	.	.	.	.	.	
													.	.	.	.	37	.	.	.	.	55		
														.	.	.	.	42	.	.	.	.		
															.	.	.	.	.	.	.			

G. swynnertoni

January	February								March								April							
29	1	5	8	12	16	19	22	26	1	5	8	12	15	19	22	26	29	2	6	10	13	16	19	24	27
to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to
31	3	7	11	14	18	21	24	28	3	7	10	14	17	21	24	28	31	5	8	12	15	18	23	26	29
	31	23	24	15	29	21	19	11	6	10	21	8	15	33	12	33	57	77	65	57	41	13	40	35	49
		21	12	12	3	21	28	9	8	11	10	13	12	.	19	.	26	12	16	57	37	28	12	10	18
			8	7	8	5	15	19	11	16	4	15	13	.	.	26	.	.	61	7	43	35	16	24	12	
				12	10	5	2	13	4	7	5	9	9	6	6	.	9	.	.	.	.	23	14	31	23	
					5	5	3	.	10	11	.	6	10	5	.	.	.	5	.	.	.	9	17	7	.	
						3	.	2	2	2	9	.	.	.	5	.	.	7	.	.	.	.	.	24	18	
							3	5	.	.	.	11	.	.	.	.	.	.	.	.	.	.	.	.	.	
								.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
									.	.	2	.	.	9	.	.	.	.	.	.	.	.	.	.	
										.	.	6	.	.	.	.	.	6	.	.	.	.	.	.	
											.	.	.	.	.	.	.	.	.	.	.	.	.	.	

Note. These tables are made from Table 3 by correcting to a constant catch (100) per half-week period. Thus in the *morsitans* table, 56 were released on 29–31 January and 26 were caught on 1–3 February, including eight recaptures; $\frac{8\times100\times100}{56\times26}=55$ approximately, the first figure in the *morsitans* table above.

Population is calculated, for *swynnertoni* for example on 1–3 February, from

$$\frac{100\times100(21+8+12+5+3+3)}{31(23+12+7+10+5+5)}=270 \text{ approximately.}$$

Actually it is best to take reciprocals of the populations and then smooth by working $\frac{1}{2}(a+b)$. Monthly means can be calculated from the means of such smoothed reciprocals. Death-rates are found by taking, for example, in the *swynnertoni* table $1-\frac{21+8+12+5+3+3}{23+12+7+10+5+5}=0{\cdot}16$, or 16% per half-week. For the whole table, the numerators and denominators of the 24 successive fractions are added to give $\frac{1171}{1833}=0{\cdot}6388$; this value is squared to give 0·4081, which subtracted from unity gives a death-rate of 0·5919 per whole week. The reciprocal of this death-rate (which includes emigration), is the mean life within the marking area, namely 1·689 weeks, or 11·8 days.

	Caught before, on and after date shown			Caught before and after date shown			Total catch			Caught before, on and after date shown			Caught before and after date shown			Total catch		
Date	Feb.	Mar.	Apr.	Feb.	Mar.	Apr.	Feb.	Mar.	Apr.	Feb.	Mar.	Apr.	Feb.	Mar.	Apr.	Feb.	Mar.	Apr.
1	10	8	—	60	62	—	15	15	—	4	2	—	31	45	—	26	30	—
2	4	16	32	82	51	76	5	18	13	—	—	7	42	42	23	8	33	18
3	4	6	—	88	46	—	6	19	—	2	1	—	43	54	—	11	18	—
4	—	—	14	—	—	70	—	—	12	—	—	8	—	—	36	—	—	17
5	14	—	6	87	51	68	12	13	8	1	5	4	44	50	37	18	33	11
6	13	1	3	82	50	66	29	3	9	6	7	7	43	50	36	47	21	16
7	13	7	5	97	41	69	22	19	5	7	1	8	60	44	43	26	29	14
8	19	6	23	100	54	60	24	6	12	3	8	16	53	47	41	27	20	25
9	—	5	—	—	51	—	—	11	—	—	7	—	—	44	—	—	24	—
10	13	10	10	87	54	56	28	7	8	5	4	7	50	39	44	33	23	12
11	16	—	8	96	—	52	23	—	8	3	—	7	43	—	45	38	—	6
12	22	10	12	88	45	48	34	13	11	4	3	18	46	34	43	26	21	24
13	15	14	4	104	40	54	12	15	7	7	6	7	55	27	46	24	22	20
14	6	12	13	109	55	58	10	8	11	8	2	21	49	27	45	42	11	22
15	—	5	10	—	53	58	—	13	6	—	2	4	—	23	44	—	7	14
16	12	6	9	108	48	55	9	17	7	5	6	7	53	16	40	24	40	16
17	19	8	8	103	49	53	20	13	5	10	3	6	58	14	35	18	24	24
18	16	—	13	116	—	47	15	—	16	13	—	10	60	—	31	16	—	29
19	8	—	8	115	53	40	12	9	12	9	—	3	63	20	28	15	12	26
20	10	6	11	116	54	36	18	6	9	12	2	1	59	16	28	15	9	10
21	32	6	—	113	49	—	30	7	—	2	1	—	57	14	—	26	11	—
22	25	3	—	101	50	—	33	5	—	10	2	—	56	13	—	23	11	—
23	16	12	11	102	49	29	15	10	13	12	1	2	49	13	24	44	13	12
24	9	15	7	94	54	24	9	12	10	5	—	6	48	14	18	26	10	22
25	—	—	4	—	—	18	—	—	7	—	—	4	—	—	17	—	—	16
26	6	15	2	87	60	13	12	9	6	7	—	1	52	13	12	22	5	11
27	8	9	1	79	62	9	15	10	5	3	1	1	53	14	11	17	11	9
28	6	18	—	72	87	7	8	7	4	2	7	1	50	18	9	24	9	9
29	Jan.	1	—	Jan.	84	—	Jan.	4	—	Jan.	2	—	Jan.	18	—	Jan.	14	—
30	2	2	—	15	79	—	16	9	—	—	3	—	10	17	—	25	20	—
31	2	23	—	30	83	—	29	6	—	—	—	—	22	22	—	30	15	—
Total	320	224	214	2331	1514	1066	461	284	204	140	76	156	1249	748	736	651	496	383
Days							26	27	23							26	27	23

The figures in the middle columns of the table are easily found from tables similar to Table 3, but set out by single days instead of by half-weeks. To find the recaptures marked before, and recaught after, any particular day, draw an isosceles triangle with its right-angled apex directly below the date in question and on a level with the first row of figures in the table, and add the figures contained in the triangle, whose base is far enough down to include all possible recaptures. Thus supposing for the moment that Table 3, *morsitans* section, were arranged by days not half-weeks, we should add for the date February 8–11: 13; 6, 2; 6, 3, 4; 3, 6, 5; 3, 4, 2; 3, 2, 4; 2, 1, 0; 2, 3, 0; 3, 1, 0. In this case of course the left-hand corner of the isosceles triangle enclosing these figures is empty because the date chosen is near the commencement of the observations.

From this table we calculate the January–February *morsitans* population as $\frac{2331 \times 461}{320 \times 26} = 129$, for March $\frac{1514 \times 284}{224 \times 27} = 71$, etc.

Table 6. *First, second and later captures of individual flies (NT males) marked January–February 1951*

Capture ...	1	2	3	4	5	6	7	8	9	10
morsitans	221	130	79	47	22	14	6	5	3	0
swynnertoni	457	153	51	21	13	5	2	1	0	0
					Percentage recaptured					
morsitans	59	61	59	47	64	43	83	60	0	—
swynnertoni	33	33	41	62	38	40	50	0	—	—

THE ECOLOGY OF THE LOUGH INE RAPIDS WITH SPECIAL REFERENCE TO WATER CURRENTS

IV. THE SEDENTARY FAUNA OF SUBLITTORAL BOULDERS

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(With 25 Figures in the Text)

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INTRODUCTION

Lough Ine is a sea lough in Co. Cork, Ireland. It is joined by a narrow channel, known as the Rapids, to Barloge Creek, which in turn opens into the Atlantic. In previous papers of this series an account has been given of the strong currents set up in the Rapids by the rise and fall of the tide (Bassindale, Ebling, Kitching & Purchon 1948), and of the influence of these currents on the physical and chemical conditions of the sea water in various parts of the Rapids area (Kitching, Lilly, Lodge, Sloane, Bassindale & Ebling 1952). This paper contains the results of a survey of the distribution of animals adhering to sublittoral boulders in the same area.

Fig. 1 is a map of the Rapids, showing the position of all stations, features and shore marks mentioned in this paper; a detailed chart has already been published (Bassindale *et al.* 1948). Stations are known by the names of nearby features or shore marks. The station known as 'Harbour' is outside the small boat harbour, as indicated. The Sill, which is the shallowest and narrowest part of the Rapids, extends from mark 4 to mark 7. The depth of water at the lowest tide is 1·3 m. in the deepest part of the channel off mark 1, 0·5 m. on the Sill, and 3 m. between Nita's Rock and Poleen. The bottom of the Rapids is covered with a dense forest of laminarian seaweeds, mainly *Saccorhiza bulbosa* de la Pyl. Boulders extend from the Rapids along both shores of the lough, but at depths greater than a few metres they are covered with mud. Also boulders extend along both shores from the Rapids southwards, but the bottom is mainly sandy in mid-channel between Nita's Rock and Poleen.

Our observations of the environmental conditions, made during July, have led to the following conclusions:

(1) The current is fastest on the Sill, where it reaches 3 m./sec. It diminishes northwards and southwards from the Sill, but is still strong at the surface far beyond

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the limits of the map (Fig. 1). The current falls off from the surface downwards, with a sharp decrease at the level of the canopy of laminarian fronds. Off the north end of the quay (mark 1) it is negligible near the bottom, but on the Sill it is still considerable, especially over the surface of large upstanding boulders.

(2) Over most of the Rapids area the temperature of the water changes with the tide, the incoming water being colder, in July, than that flowing out. But at certain stations at the north end of the Rapids the temperature remains high during inflow because surface lough water is drawn continually across them by eddies. This is true of Codium Bay, Renouf's Bay, and to a smaller extent of Harbour.

(3) There are broken shells and shingle in crevices between boulders on the Sill, but there is very little fine sediment. The deposit of mud on the tops of boulders, and among the seaweeds and animals attached to them, becomes greater where the current

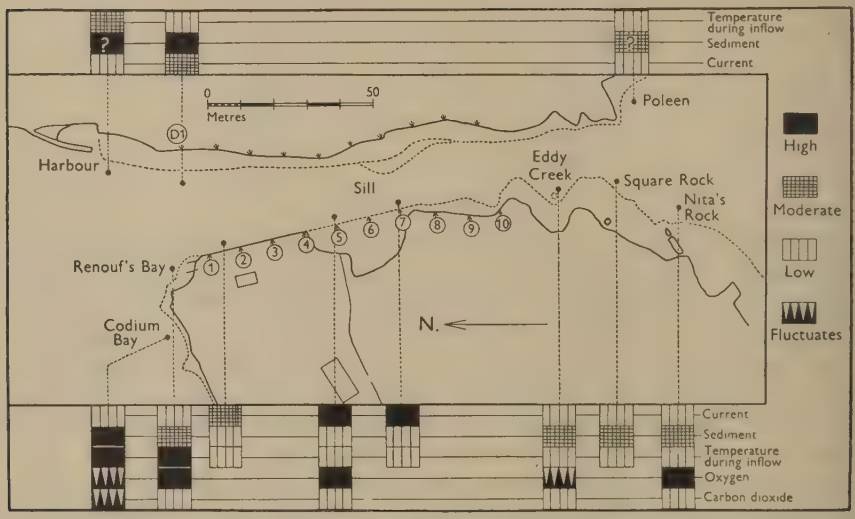

Fig. 1. Map of the Rapids area, showing diagrammatically the environmental conditions at stations mentioned in this paper.

is less. In sheltered bays the total dry weight of sediment on the tops of boulders reaches 15–40 g. per 1000 sq.cm. of surface. On the bottoms there is much less, and there are no significant differences between stations.

(4) The oxygen and carbon dioxide tension of the water remain steady throughout the day in the main stream of the Rapids. This is also true of Renouf's Bay, where there is a continual gentle current reaching to the bottom. In other sheltered bays the tensions of oxygen and carbon dioxide fluctuate diurnally, no doubt owing to the photosynthetic activity of algae. Low oxygen content and high acidity at night are probably partly due, at least in Codium Bay, to the reducing power of the mud.

(5) The salinity in July (34·7–35·3‰) is in the range characteristic of open coastal water. No significant differences in salinity were found at any one time between the bottom waters at different stations, even after heavy rain.

Conditions not encountered in July may well play an important part in the ecology

of the Rapids. In spite of this and other obvious limitations and imperfections, we shall try to use this description of the environment to explain our observations on the distribution of animals. There are sufficient different combinations of environmental conditions at the various stations, as shown in Fig. 1, to provide a useful though incomplete natural experiment. The conclusions drawn must be regarded as working hypotheses, to be tested in future observations and experiments.

METHODS

Boulders were collected in July 1948 from stations throughout the Rapids area, and as far as possible the quantities of all attached animals were estimated. Another set of boulders was collected in July 1950, but these were examined only for certain groups or species about which we needed more information. At all the places from which boulders were collected there is a depth of about 1 m. at the lowest tide, except on the southern edge of the Sill, off mark 7, where there is about 0·5 m. The tops of some very large boulders on the southern edge of the Sill were examined by diving at slack water in July 1949, because they were too big to move.

The surfaces of boulders were completely stripped during their examination in the laboratory. Tops, sides and bottoms were treated separately. Sides were examined only if they were vertical, and any surfaces less than 100 sq.cm. in area were rejected. At some stations the number of acceptable sides was rather small. The area of each boulder surface was determined by measurement. The quantities of colonial animals were usually estimated by the percentage area of surface covered, and solitary animals were counted. The lithological nature of the boulders collected in 1948 was determined by Dr Desmond Donovan, of the Department of Geology, University of Bristol.

Material was identified as far as possible at Lough Ine, but a considerable collection was kept for subsequent confirmation. Procedure for the various groups was as follows:

PORIFERA. All material was preserved in alcohol. Many specimens were examined by Prof. L. P. W. Renouf. The complete collection (over 1300 specimens) was identified by Dr M. Burton of the British Museum (Natural History).

HYDROZOA. Identified from Hincks (1868) by R.B.

ANTHOZOA. Left to expand in sea water and identified alive from Stephenson (1935) by R.B.

SERPULIDAE. Decalcified after examination in tube; identified from Fauvel (1927) by R.B., with assistance in 1950 from Mr J. Peters.

CIRRIPEDIA. Identified by R.B.

MOLLUSCA. Identified from Forbes & Hanley (1853) and Winckworth (1922) by S.J.L., with assistance for Anomiidae from Miss Anne Legg. Placophora were checked by Mr G. L. Wilkins of the British Museum (Natural History) and *Patella* spp. by Dr R. G. Evans of the University College of North Staffordshire. The nomenclature used is that of Winckworth (1932).

POLYZOA. Material was mounted on microscope slides in de Faure's medium or Canada balsam, or dry on wooden slides or blocks. Samples of all species found were identified by Dr Anna B. Hastings of the British Museum (Natural History), mainly in accordance with Marcus (1940). The main collection was identified in accordance with these by J.A.K., with assistance in 1950 from Mr M. A. E. Mortimer.

TUNICATA. All material was preserved in alcohol and identified by Miss Marjory Murphy of the Department of Zoology, University College, Cork. The nomenclature is that used by Berrill (1950).

RESULTS

The results of the lithological examination of boulders made in 1948 are summarized in Fig. 2. According to Dr Donovan's report, except for one boulder of hard purple siltstone of unknown origin, all the boulders were of the local Devonian rock through which the Rapids are cut. This consisted originally of sandstone and shales, but has suffered slight metamorphism so that the shales have become slates. The sandstones consist principally of quartz grains, with a small quantity of felspar in some cases. None of the rock types are calcareous. The sandstone forms subangular boulders of

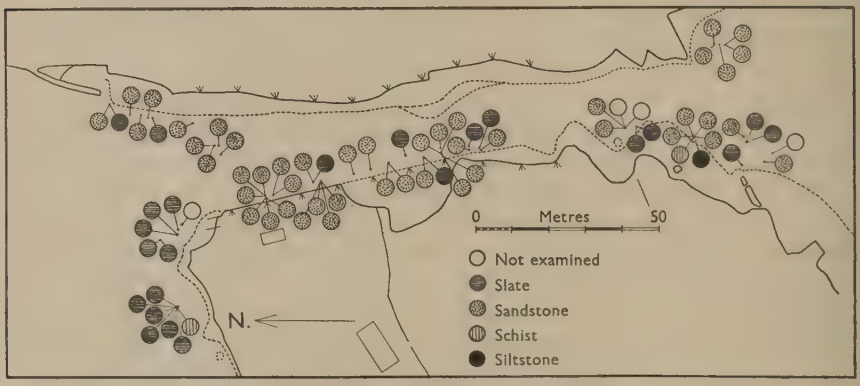

Fig. 2. Chart showing the lithological nature of the boulders collected in 1948.

various shapes; the slate forms flat slabs. The boulder surfaces examined ranged from 110 to 3500 sq.cm. in area.

The results of the examination of the fauna are summarized in Figs. 4–25, Tables 2 and 3, and in the Fauna list, all in the Appendix. Figures are given for those species which occur sufficiently often and in sufficient quantity to justify the representation of population density by grades. Data for species which occur fairly frequently but only in small quantities are given in the tables. The records of infrequent species are given directly in the Fauna List, which also includes the full names of all species referred to in this paper, with reference to any figures or tables in which they are mentioned.

A summary of the distribution of the commoner species in the Rapids area is given in Table 1, which is based on the data given in Figs. 4–25 and Tables 2 and 3. In it the species are classified somewhat arbitrarily in accordance with preference for tops or bottoms of boulders and for the main stream or sheltered bays. Those species showing no obvious preference have been classified as such, even though some small degree of preference may in fact occur. Of the species recorded in this paper, forty-nine were considered to show a clear enough pattern of distribution for inclusion in

the table. For the others, more records are needed. There is no obvious correlation between the distribution of species and the lithological nature of the boulders.

DISCUSSION

Those animals which are distributed unequally in the Rapids area are distributed in accordance with water current and sediment. For instance, in general the same species are found in Codium Bay, Renouf's Bay, Eddy Creek, off Square Rock and Nita's Rock,

Table 1. *The distribution of the commoner species*

Preference for tops	No obvious preference for tops or bottoms	Preference for bottoms
	Preference for main stream	
Tubularia bellis	*Sertularia operculata*†	
*Patella vulgata**	*Plumularia setacea*†	
*Patella aspera**	*Sagartia elegans*‡	
	Metridium senile	
	Corynactis viridis§	
	Balanus crenatus	
	Costazia costazii	
	Hippothoa hyalina	
	Umbonula littoralis†	
	Mytilus edulis‡	
	No obvious preference for main stream or sheltered bays	
Acmaea virginea	*Myxilla rosacea*	*Haliclona limbata*
	Amphilectus fucorum	*Leuconia nivea*
	Halichondria bowerbanki	*Hymedesmia bronstedi*¶
	Pomatoceras triqueter	*Spirorbis* spp.
	Balanus balanus	*Escharoides coccinius*
	Verucca stroemia	*Diastopora patina*
	Scruparia chelata†	*Schizomavella* spp.
	Scrupocellaria reptans¶	*Lichenopora hispida*
	Crisia eburnea	
	Tubulipora plumosa	
	Musculus marmoratus	
	Hiatella arctica	
	Kellia suborbicularis	
	Monia squama	
	Heteranomia squamula	
	Didemnum maculosum	
	Preference for sheltered bays	
Acanthochitona crinitus	*Haliclona indistincta*	*Serpula vermicularis*
	Adocia cinerea	*Bugula flabellata*
	Mycale rotalis	*Escharella variolosa*
	Anthopleura belli	*Membraniporella nitida*
	Caryophyllia smithi	
	Cellepora pumicosa	

* Confined to upper surfaces of large boulders in full current on Sill.
† Possibly prefer tops.
‡ Mainly on Sill.
§ Extends into some shelter, and prefers bottoms on Sill.
¶ Not on Sill.

in Poleen, and at Harbour—all stations which are sheltered from current and rich in sediment, but which differ among themselves as to water temperature, oxygen tension and carbon dioxide tension. Other species are confined to the main stream of the Rapids, although very similar conditions of temperature (at least in July) are found at

sheltered stations south of the Sill. Some of the effects of current and sediment are suggested in Fig. 3. According to this scheme current may exert a number of direct effects upon the animals living on boulders, and also may influence them indirectly by preventing sedimentation. The designation of effects as favourable and unfavourable is of course arbitrary. A preference for strong current could be explained in terms of the effects listed in the top right of this diagram, which might render a region of strong current favourable, and of those in the bottom left, which might render a region of weak current unfavourable. Conversely, a preference for weak current might be explained in terms of the effects in the bottom-right and top-left corners.

A few large boulders on the Sill project upwards to the level of the laminarian canopy and are swept by a strong current. Their upper surfaces are clean except for a smooth

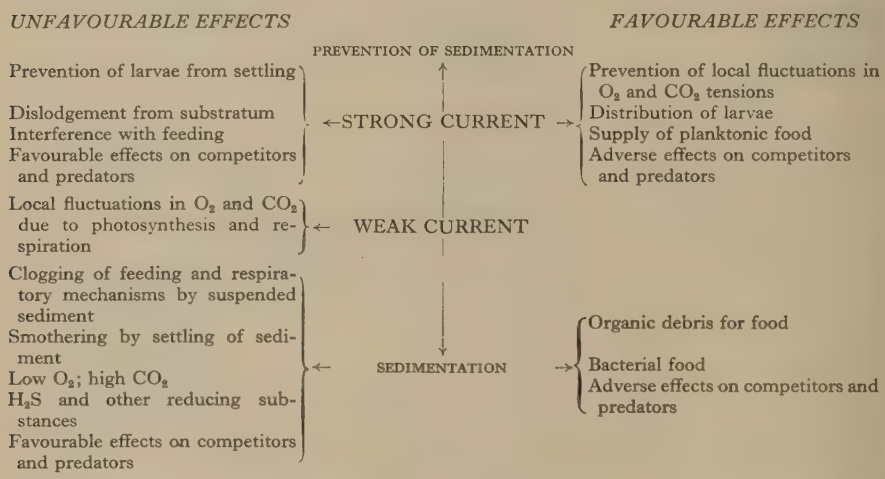
UNFAVOURABLE EFFECTS
FAVOURABLE EFFECTS
PREVENTION OF SEDIMENTATION
Prevention of larvae from settling
Dislodgement from substratum
Interference with feeding
Favourable effects on competitors and predators
←STRONG CURRENT→
Prevention of local fluctuations in O_2 and CO_2 tensions
Distribution of larvae
Supply of planktonic food
Adverse effects on competitors and predators
Local fluctuations in O_2 and CO_2 due to photosynthesis and respiration
← WEAK CURRENT
Clogging of feeding and respiratory mechanisms by suspended sediment
Smothering by settling of sediment
Low O_2; high CO_2
H_2S and other reducing substances
Favourable effects on competitors and predators
← SEDIMENTATION →
Organic debris for food
Bacterial food
Adverse effects on competitors and predators

Fig. 3. Diagram representing the influence of water current on other environmental conditions.

coating of encrusting coralline algae, occasional *Patella* spp., and some small *Mytilus edulis* in crevices. Both *Patella* spp. and young *Mytilus edulis* are common on rocky shores exposed to severe wave action. *Patella* is normally restricted to rather bare surfaces; it probably cannot crawl about where there is any considerable growth. Strong current probably resembles wave action in keeping the space clear.

Those species which show a preference for the main stream of the Rapids evidently occupy an intermediate habitat, being excluded from the most current-swept boulders by mechanical effects and from sheltered bays by means to be discussed. This condition has already been described for *Patina pellucida* (Ebling, Kitching, Purchon & Bassindale 1948). The limits of tolerance naturally vary from species to species. For instance after *Patella*, *Mytilus edulis* (Fig. 17) is the most resistant to current, but does not colonize the sheltered bays, whereas *Corynactis viridis* (Fig. 10) appears to find the current too strong on the Sill except under boulders, but penetrates some way into shelter. Except for the hydroids, most of the species preferring the main stream are almost equally plentiful on the bottoms and on the tops of boulders. The current under boulders must be very slight, even on the Sill. Therefore we cannot attribute the

survival of these species to the suppression of their competitors by a mechanical effect of current, although this might keep away motile predators (see p. 94). A number of other possible mechanisms remain, and it is likely that several of them combine to produce the distribution observed. In the main stream of the Rapids a very weak current at the bottom would help to dissipate the products of respiration, excretion, and photosynthesis, whereas in sheltered bays local chemical changes would be accentuated by stagnation or modified by the reducing action of accumulated organic material. We have not yet investigated the 'microclimate' surrounding boulders; chemical changes in a layer of water very close to the boulders would not have been detected in our hydrographical investigation. Other possible agents are the accumulation of particles in the water near the bottom, and the stirring up of sediment in stormy weather which might clog the feeding mechanisms of some animals. Direct smothering by sediment does not appear to be an important limiting factor in the case of the species under consideration. There is very little sediment on the bottoms of boulders at any station, and yet there are no species which occur equally on tops and bottoms in the main stream but only on bottoms in shelter.

The mechanical effects of current are probably not important in restricting species to sheltered stations, as these species are not found in the main stream on the under sides of boulders, where they would be protected from current. Perhaps they require a supply of organic debris or bacteria for food; this would presumably be most plentiful where sedimentation occurs. This explanation has been used by Prenant & Teissier (1924) and Prenant (1927) to account for the observation that in the neighbourhood of Roscoff a number of species are only found near deposits of mud. Fischer (1929) has stated that various littoral species on the north coast of France are found where the reducing power of the water is highest. He has tentatively interpreted this as favouring Pütter's hypothesis, but it seems possible that reducing power is correlated with the presence of organic particles.

Very few organisms were found to prefer tops. Tops are well populated by species which also inhabit the bottoms, but they do not appear to offer many exclusive advantages. *Patella* has already been discussed. It is probable that it requires a strong current to keep down competitive species and that this is only found on tops; in addition it feeds on algae. *Acmaea virginea* and *Acanthochitona crinitus* also feed on algae. The only other certain example of a preference for tops is the hydroid *Tubularia bellis*; besides this there are four possible cases—two hydroids and two polyzoa. It seems likely that the hydroids do not find enough room to grow on the under sides of boulders.

Many organisms prefer bottoms. Some of these organisms prefer sheltered bays; some are found equally in sheltered bays and in the main stream; but none prefer the main stream. The bottoms of boulders in the main stream are populated by many species, but all of them are found as abundantly in other habitats. A preference for bottoms might be caused by the sediment on the tops in sheltered bays, by the mechanical effects of current in the main stream, and by the competition of other organisms such as algae on the tops in both places. The greatest deposition of sediment was found in Codium Bay, where several species (*Balanus balanus*, Table 2; *Cellepora pumicosa*, Fig. 20), appear to be less common on tops than at other stations, although

they are still plentiful on bottoms. Deeper down the boulders are covered by a thick layer of mud, and smothering must render them uninhabitable to many species. The mechanical effects of current are considerable on the Sill, but much less in other parts of the main stream. It is not possible at present to assess their importance. The most comprehensive explanation is that on bottoms many species escape from competition with algae (including corallines) which overcrowd the tops. It is noticeable that species preferring bottoms include a number which form encrusting sheets or are closely pressed to the rock, such as encrusting Polyzoa and Serpulidae, which might easily be overgrown. A preference of encrusting Polyzoa for the under sides of stones has been noted by Prenant & Teissier (1924). The behaviour of the larvae during settling may also be important.

All the species for which there are sufficient records conform to one of the types of distribution given in Table 1, except possibly for one. The alcyonarian *Parerythropodium hibernicum*, known only from Lough Ine, is not so far as we know found south of Renouf's Bay and Harbour. We do not know what are the conditions which confine it within the lough. There may be other exceptions among the less common species, but our records are not sufficient to justify any such suggestion.

No account has been taken so far of competition and predatory habits. Undoubtedly the growth of one organism over another plays a most important part in the ecology of sublittoral boulders. It is clear that observations and experiments are needed on the growth of organisms on particular boulders. We have suggested above that species preferring the main stream and species preferring sheltered bays are restricted to their own habitats by certain environmental factors such as chemical conditions and food supply. Some members of these two groups of species may be expected to compete in the intermediate areas, and no doubt will be restricted in part by the competition. In certain cases predators must also play an important part. For instance, the gastropod *Nucella lapillus* is to be seen feeding on *Mytilus edulis* between boulders on the Sill. The temporary destruction of beds of *Mytilus edulis* by *Nucella lapillus* has been described by Fischer-Piette (1935), and the importance of predators in restricting the spread of mussels sublittorally is emphasized also by Warren's (1936) experiments. An adverse effect of current on predators such as starfish might account for the abundance of *Mytilus edulis* on the Sill.

It would be interesting to compare the distribution, in relation to environmental conditions, of various sublittoral species at Lough Ine and on other coasts. Unfortunately, although there are many records, there is not enough information about the environment. An attempt was made by Kitching, Macan & Gilson (1934) to study the distribution of organisms in a submarine gulley at Wembury Bay, South Devon, in relation to angle of slope of the rock surface, illumination, and the deposition of sediment. Many species were found to be confined, in the submarine gulley, to vertical or overhanging rock surfaces. This was attributed to the settling of sediment on upward facing surfaces, the sediment in this case being mainly sand. A number of these species, including the sponge *Amphilectus fucorum*, the hydroids *Sertularia operculata* and *Plumularia setacea*, and the barnacle *Verruca stroemia*, grow freely on the tops of boulders at Lough Ine. This difference may be due to the fact that the conditions of sedimentation are entirely different in the two places. In the Rapids, *Sertularia*

operculata and *Plumularia setacea* are restricted to the main stream, where sedimentation of any kind is slight; *Amphilectus fucorum* and *Verruca stroemia* occur also in the sheltered bays, but the sediment here is mud, not sand. The adverse effect of sand has already been noted by Prenant & Teissier (1924).

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SUMMARY

1. The tops, sides, and bottoms of a number of sublittoral boulders from various parts of the Lough Ine Rapids area have been examined, and the quantities of the various non-motile animals have been estimated. Charts, Tables, and a Fauna List of 156 species are given.

2. Thirteen species show a preference for the main stream of the Rapids; eleven prefer sheltered bays; twenty-five show no obvious preferences in this respect.

3. Five (or possibly nine) species prefer the tops of boulders; twelve prefer bottoms; twenty-eight show no obvious preference for either.

4. Failure of species to occupy current-swept boulders on the Sill is ascribed to a mechanical effect. Restriction to the main stream, with failure to occupy sheltered bays, is thought to be due mainly to an unfavourable influence of sediment, which perhaps affects the microclimate surrounding boulders or clogs feeding and respiratory mechanisms. Restriction to sheltered bays is possibly due to a better supply of organic detritus or bacterial food.

5. Preference for tops is ascribed in some cases to feeding on algae, and in others perhaps to a lack of sufficient room for growth on the bottoms. Preference for bottoms is ascribed to an unfavourable influence acting on the tops. This may be competition with algae at all stations, mechanical effect of current in the main stream only, or settling of sediment in sheltered bays.

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APPENDIX

In the Tables and Fauna List the names of stations are abbreviated as follows:

CB = Codium Bay	*NR* = Nita's Rock
EC = Eddy Creek	*RB* = Renouf's Bay
D1 = Station *D1*	*SR* = Square Rock
H = Harbour	*St* = Station

Max. denotes the maximum density of population of a species on any one boulder surface, and is followed by the station and by the surface (top, side, bottom).

In Figs. 4–25 each circle represents a boulder surface. In the case of sides, linked circles represent sides of the same boulder. For some boulders a record for side or for bottom has not been given; this is due to the fact that the conditions for examination (p. 89) were not met.

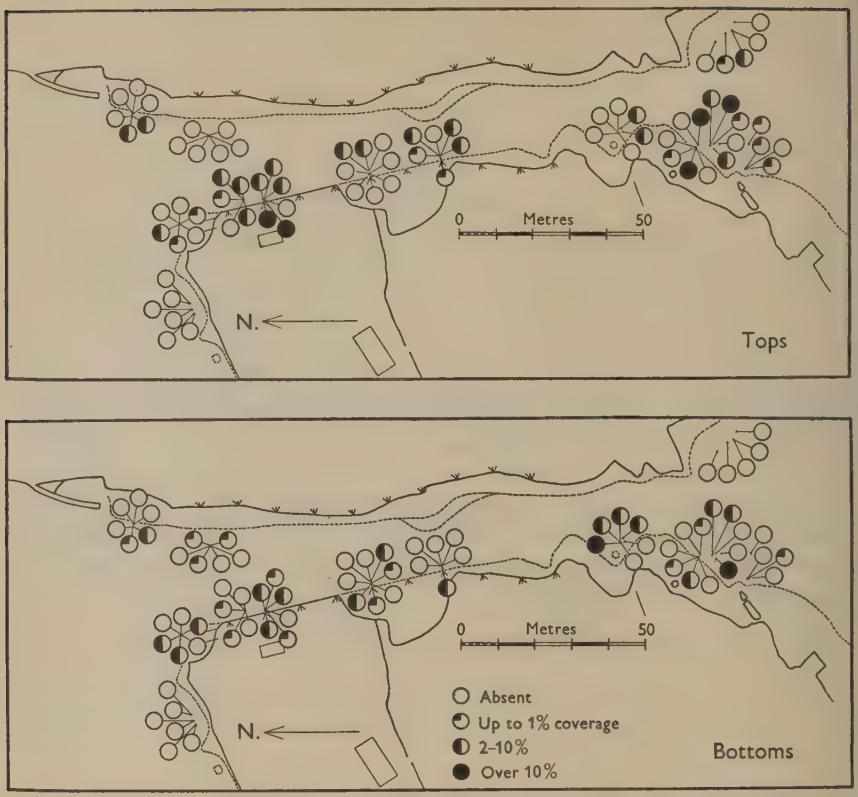


Fig. 4. Distribution of *Amphilectus fucorum* on boulders in the Lough Ine Rapids in July 1950. (Max. 20%, *SR*, top.)

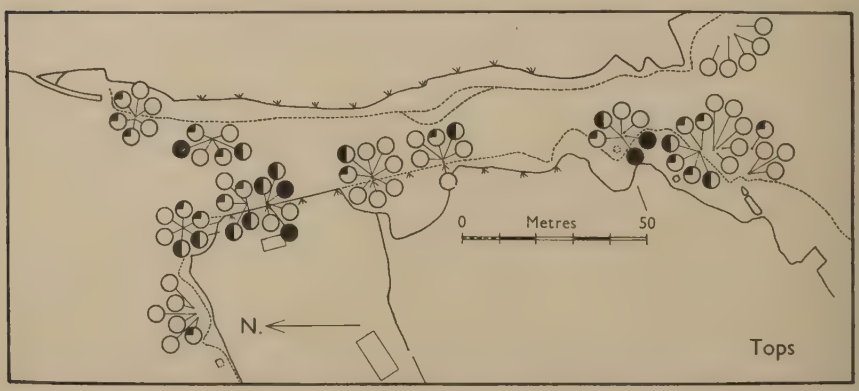
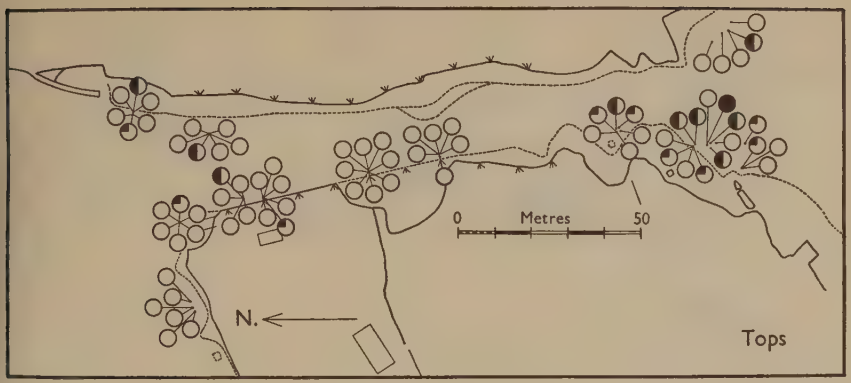


Fig. 6. Distribution of *Halichondria bowerbanki* on boulders in the Lough Ine Rapids in July 1950. (Max. 30%, *EC*, top.)



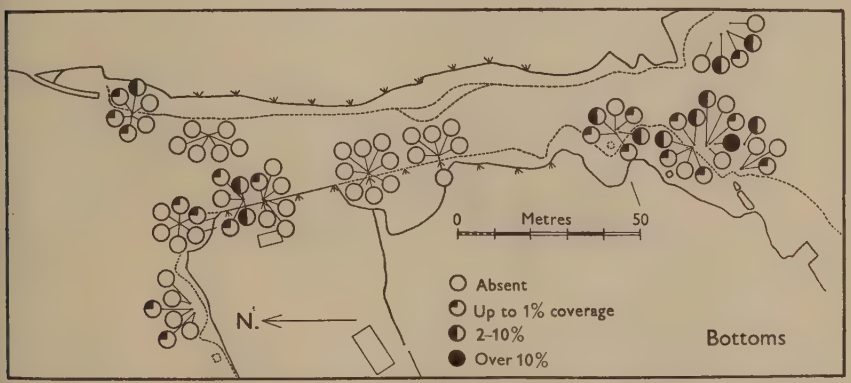


Fig. 5. Distribution of *Hymedesmia bronstedi* on boulders in the Lough Ine Rapids in July 1950. (Max. 30%, *SR*, top.)

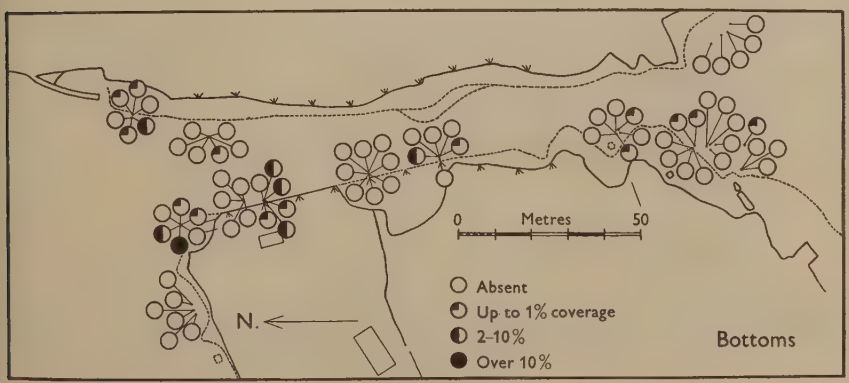


Fig. 6 (*continued*).

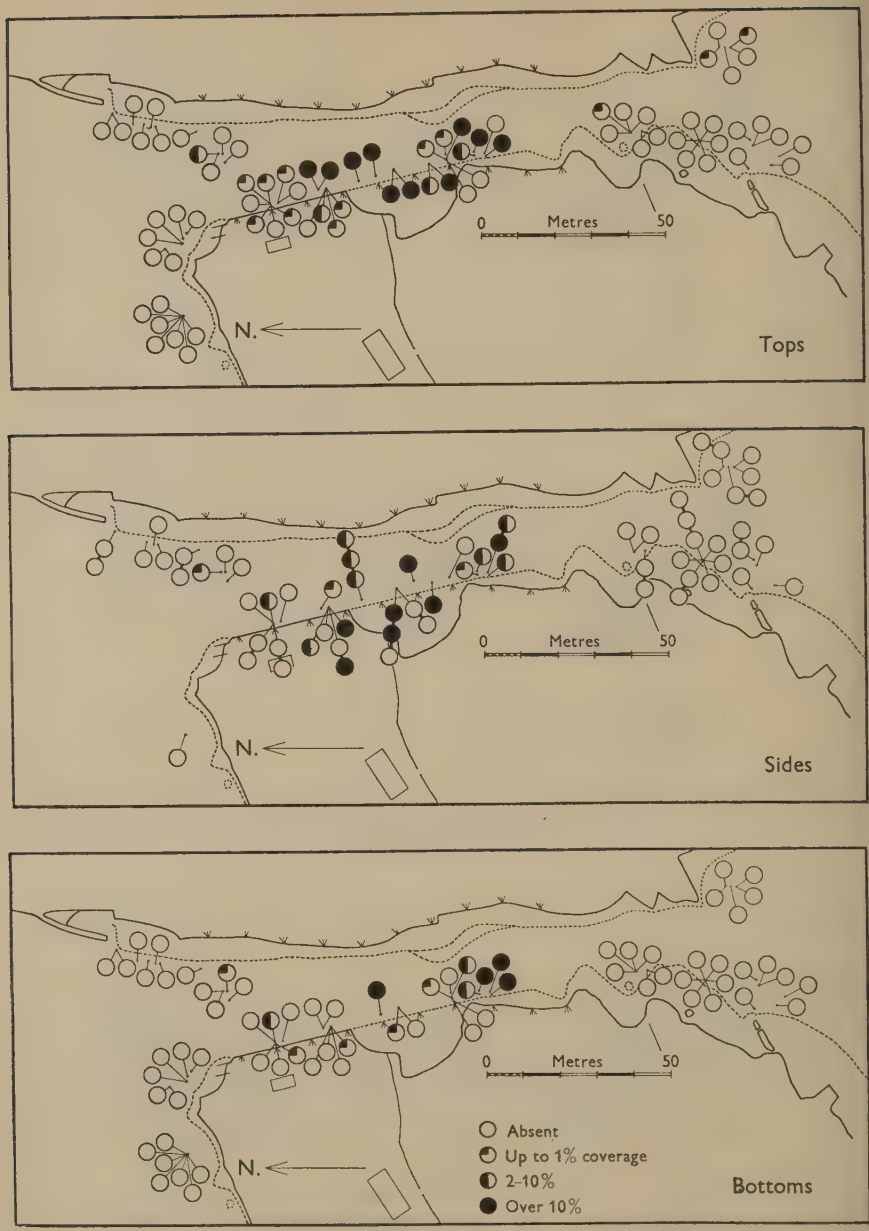


Fig. 7. Distribution of *Sertularia operculata* on boulders in the Lough Ine Rapids in July, 1948. (Max. 95%, *Sill*, top.)

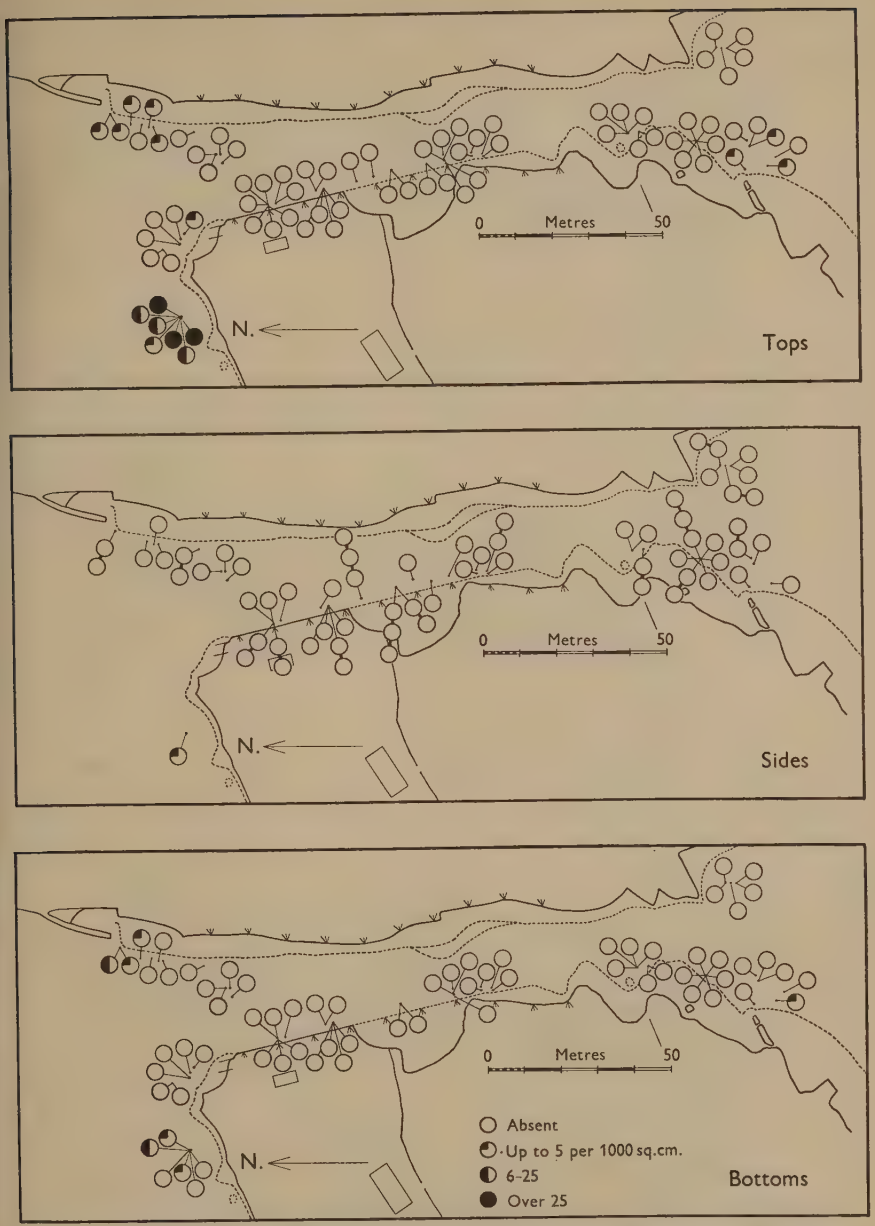


Fig. 8. Distribution of *Anthopleura ballii* on boulders in the Lough Ine Rapids in July 1948. (Max. 64 per 1000 sq.cm. *CB*, top.)

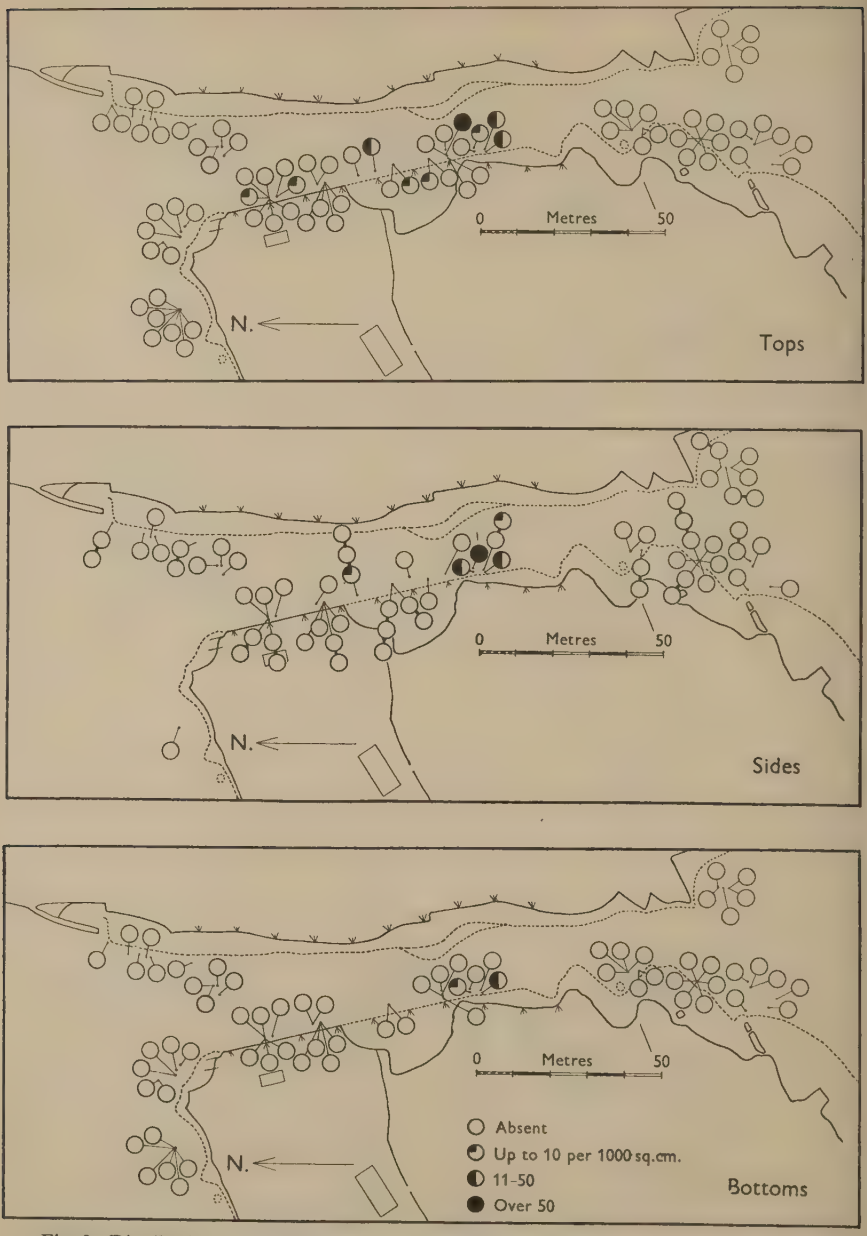


Fig. 9. Distribution of *Metridium senile* on boulders in the Lough Ine Rapids in July 1948. (Max. 87 per 1000 sq.cm., *Sill*, top.)

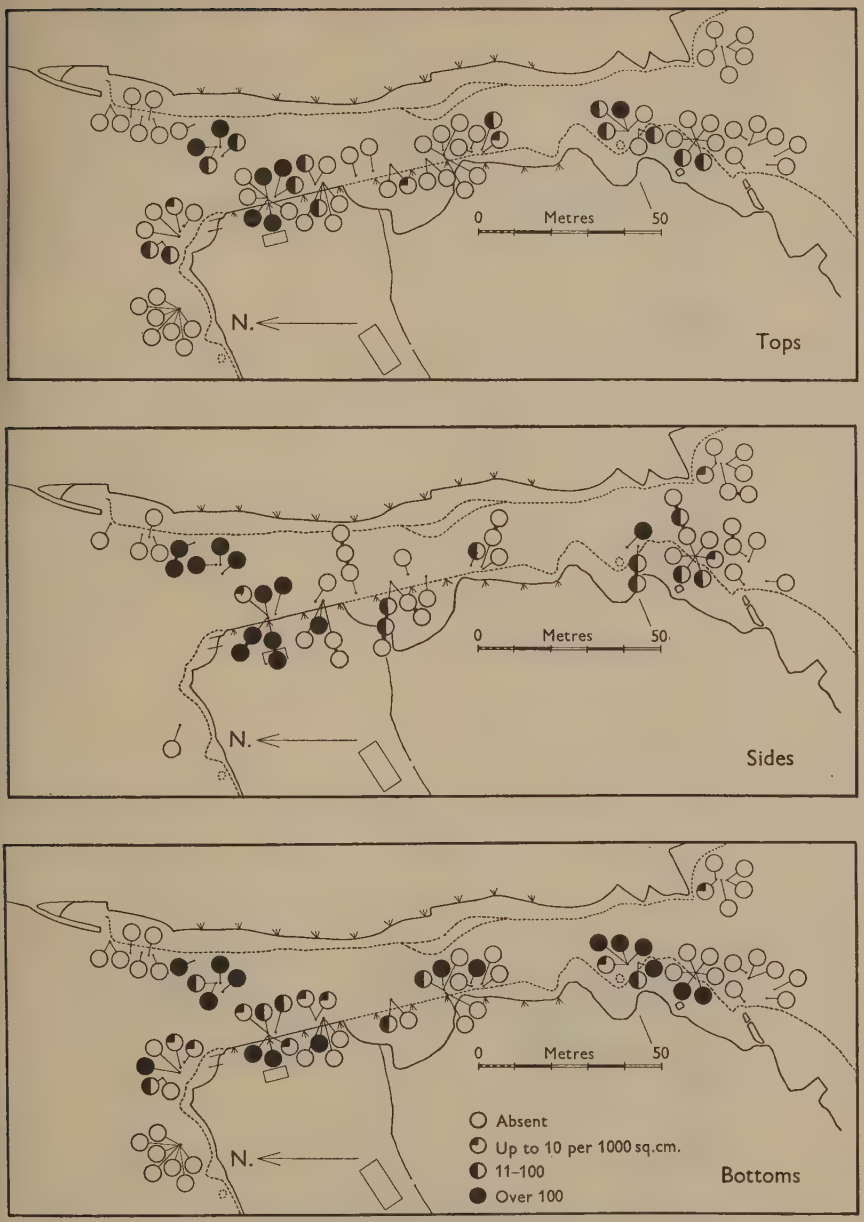


Fig. 10. Distribution of *Corynactis viridis* on boulders in the Lough Ine Rapids in July 1948. (Max. 1440 per 1000 sq.cm., *D 1*, side.)

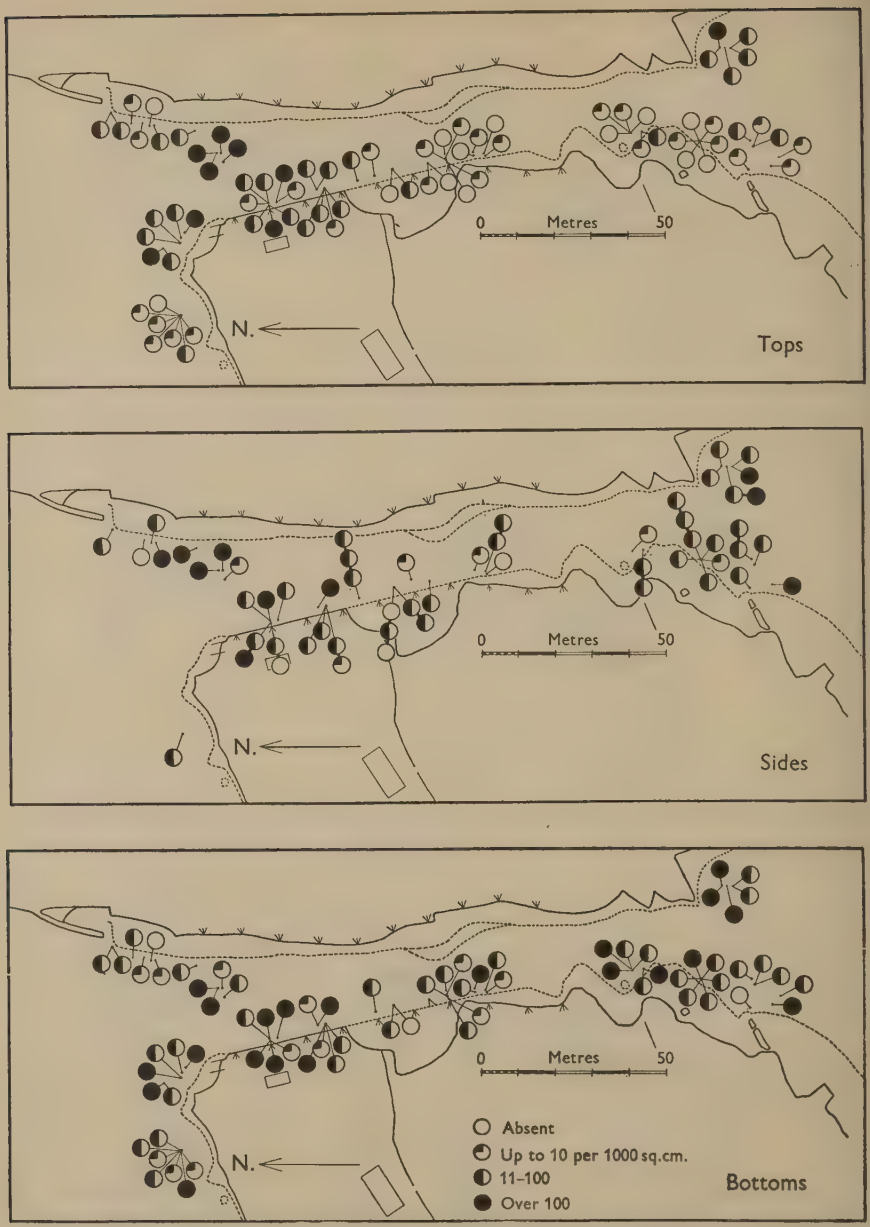


Fig. 11. Distribution of *Pomatoceros triqueter* on boulders in the Lough Ine Rapids in July 1948. (Max. 258 per 1000 sq.cm., *D1*, top.)

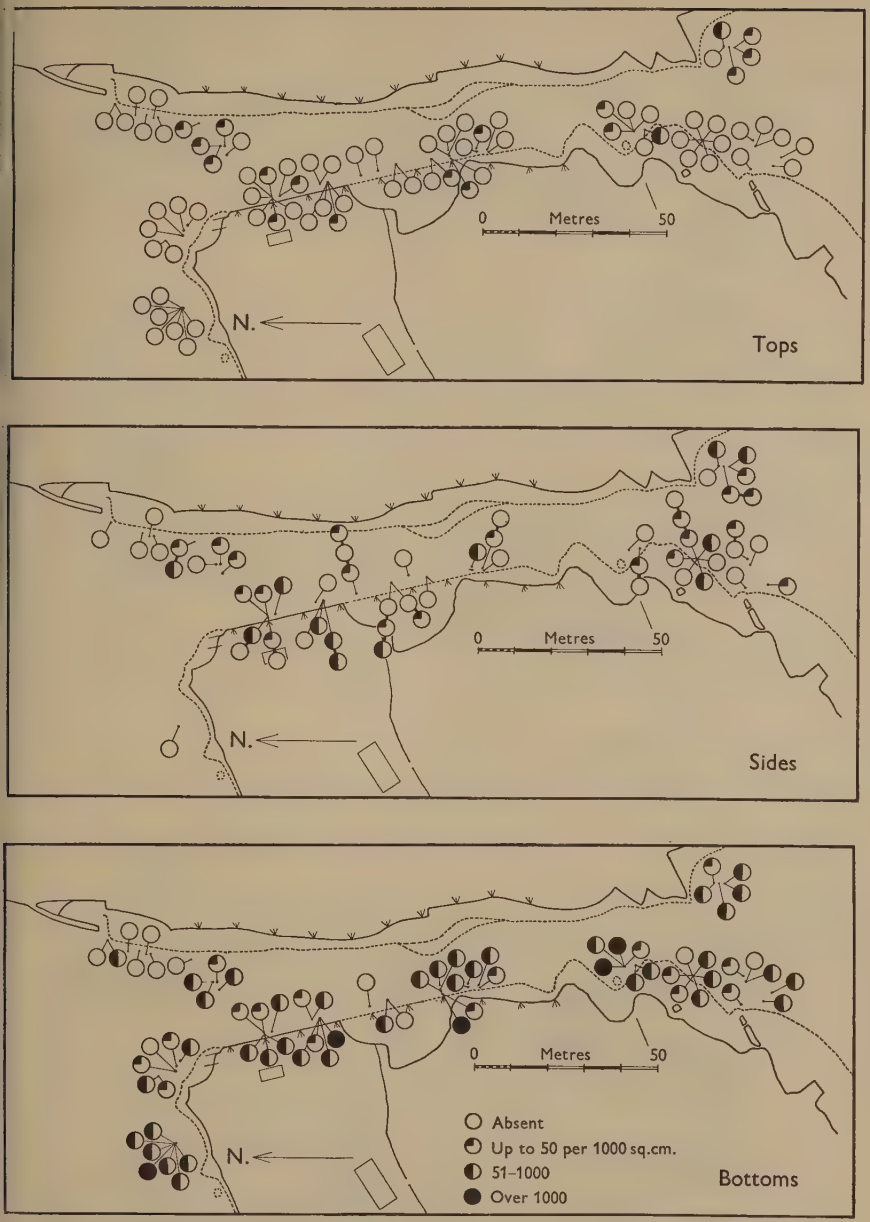


Fig. 12. Distribution of *Spirorbis* spp. on boulders in the Lough Ine Rapids in July 1948. (Max. 1770 per 1000 sq.cm., *EC*, bottom.)

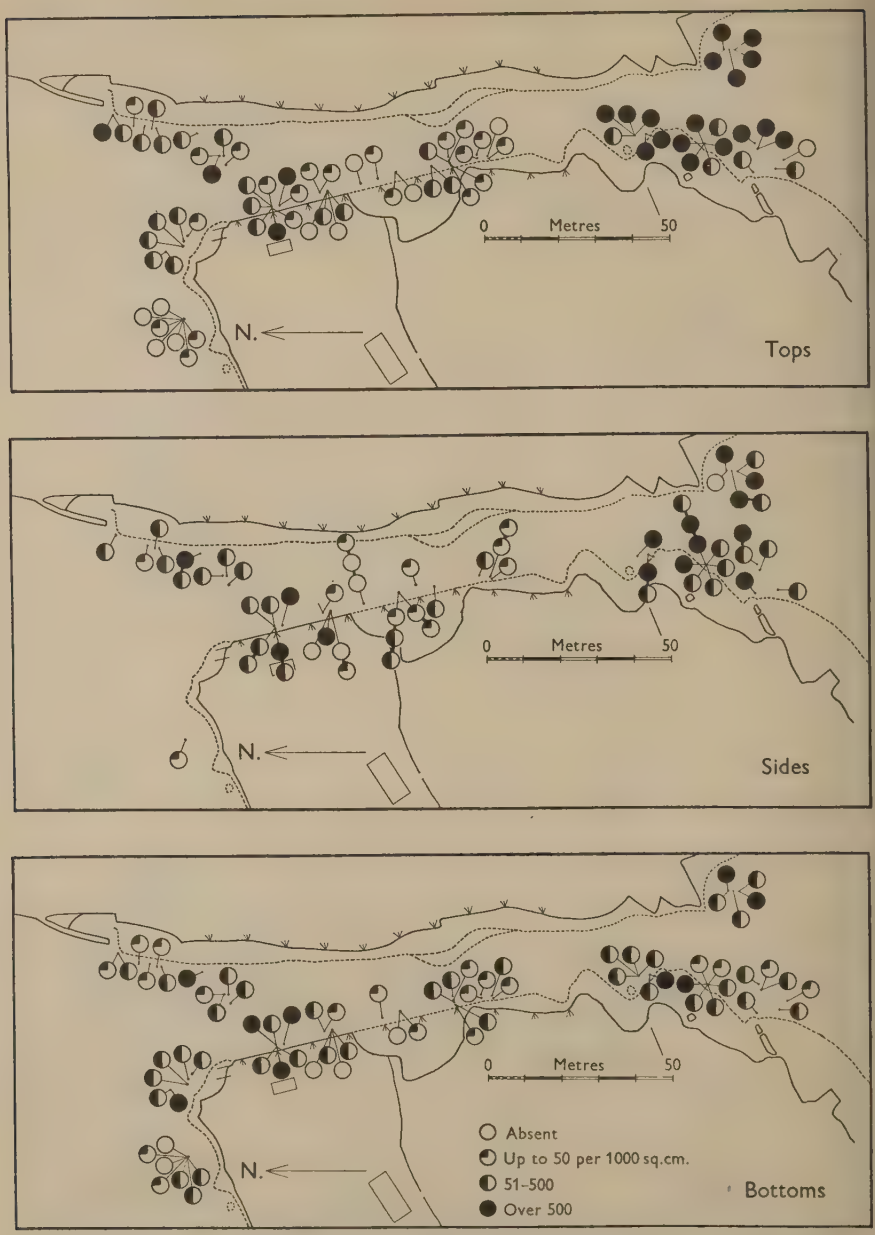


Fig. 13. Distribution of *Verruca stroemia* on boulders in the Lough Ine Rapids in July 1948. (Max. 2150 per 1000 sq.cm., *D1*, top.)

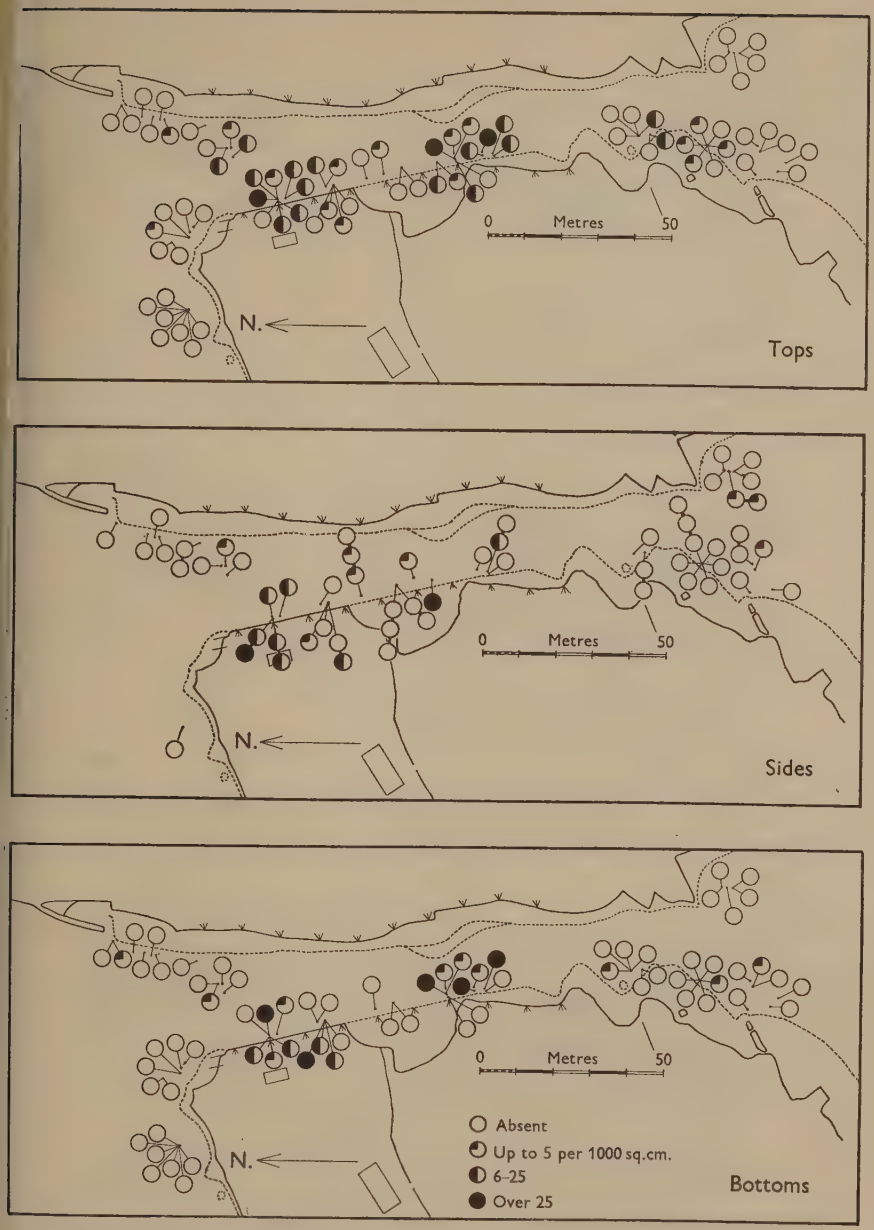


Fig. 14. Distribution of *Balanus crenatus* on boulders in the Lough Ine Rapids in July 1948. (Max. 80 per 1000 sq.cm., *St. 2*, top.)

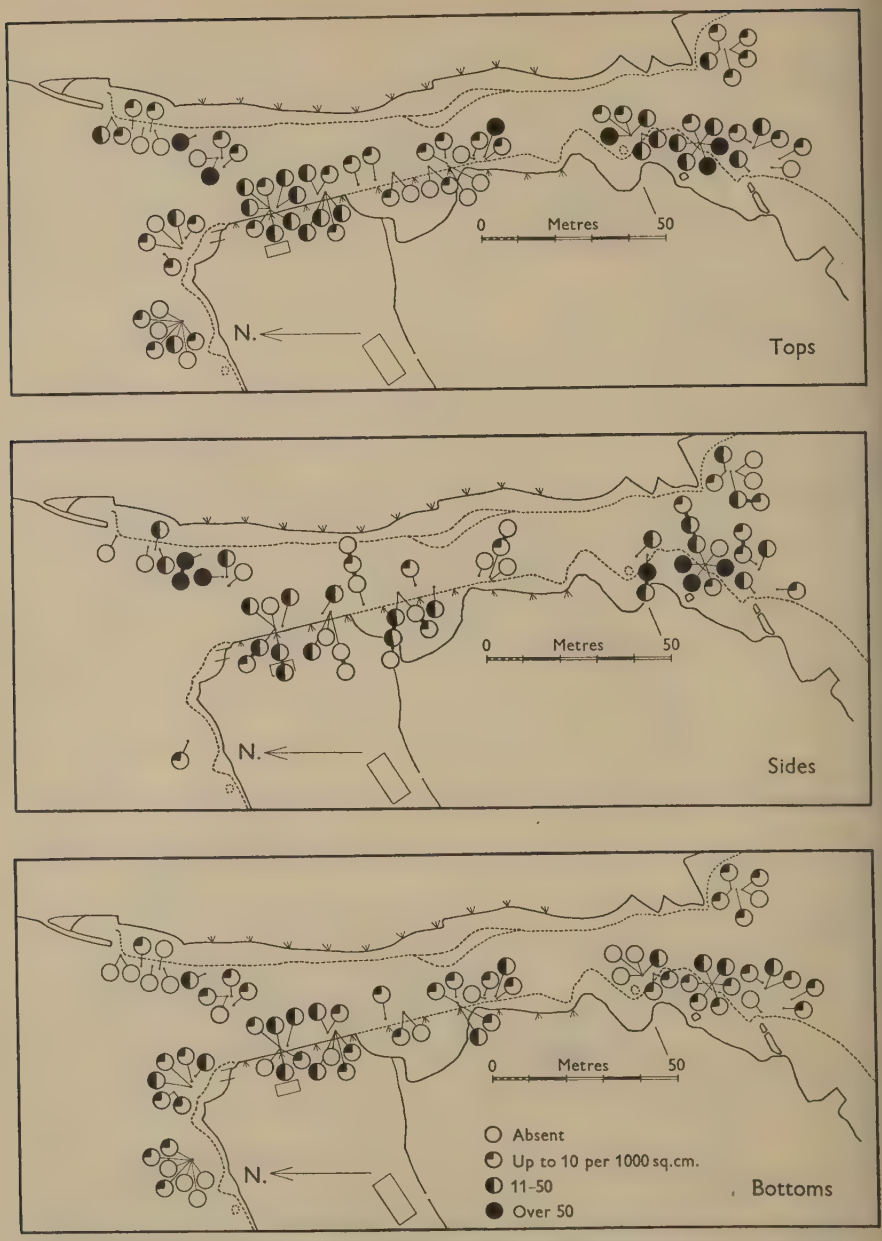


Fig. 15. Distribution of *Hiatella arctica* on boulders in the Lough Ine Rapids in July 1948. (Max. 264 per 1000 sq.cm., *SR*, side.)

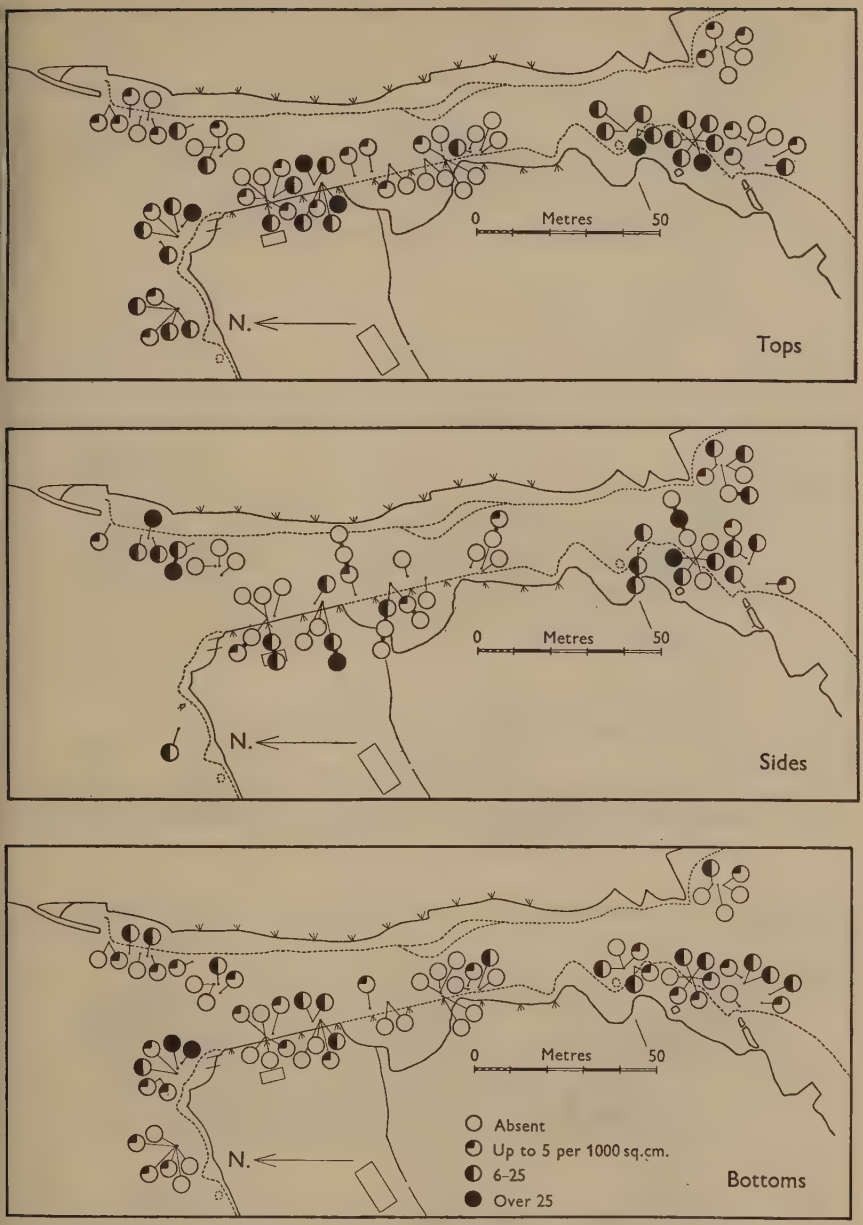


Fig. 16. Distribution of *Musculus marmoratus* on boulders in the Lough Ine Rapids in July 1948. (Max. 76 per 1000 sq.cm., *SR*, top.)

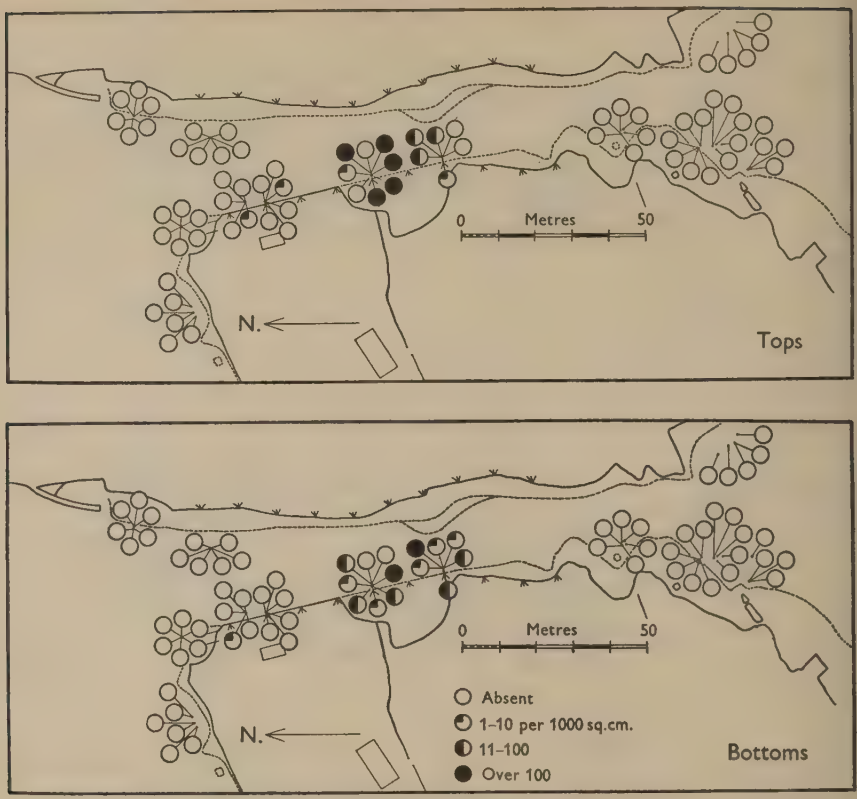


Fig. 17. Distribution of *Mytilus edulis* on boulders in the Lough Ine Rapids in July 1950. (Max. 1590 per 1000 sq.cm., *St. 5*, top.)

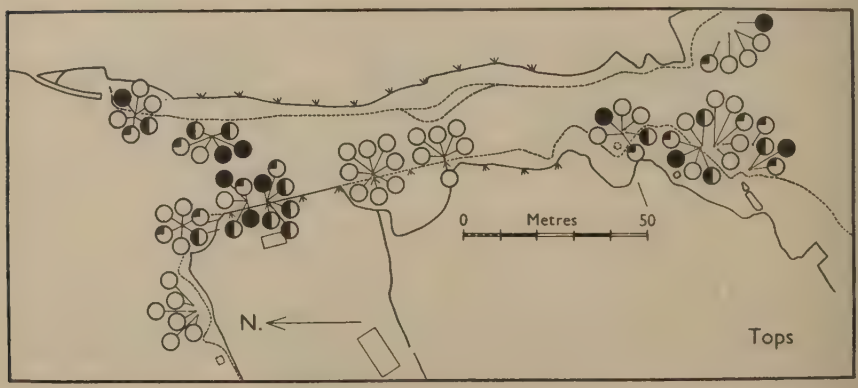


Fig. 19. Distribution of *Scrupocellaria reptans* on boulders in the Lough Ine Rapids in July 1950. (Max. 60%, *H*, bottom.)

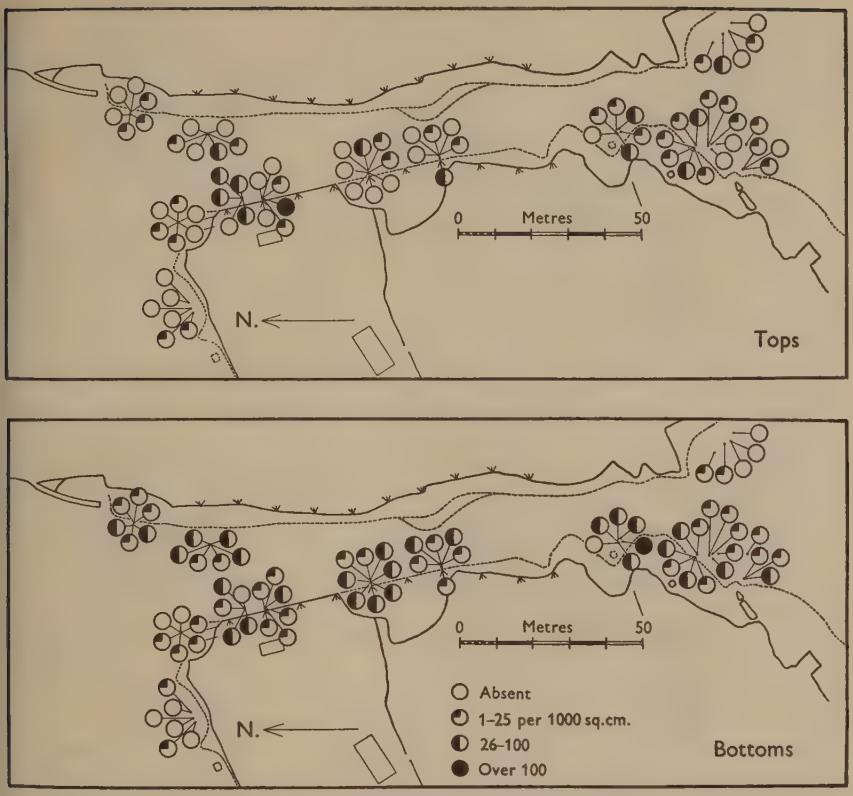


Fig. 18. Distribution of *Heteranomia squamula* on boulders in the Lough Ine Rapids in July 1950. (Max. 125 per 1000 sq.cm., *EC*, bottom.)

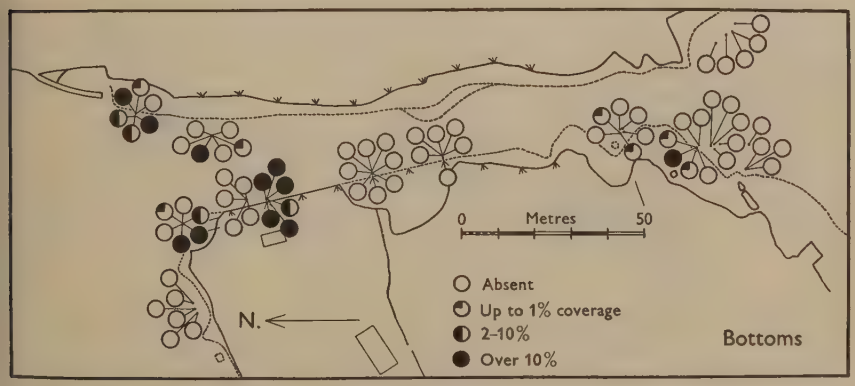
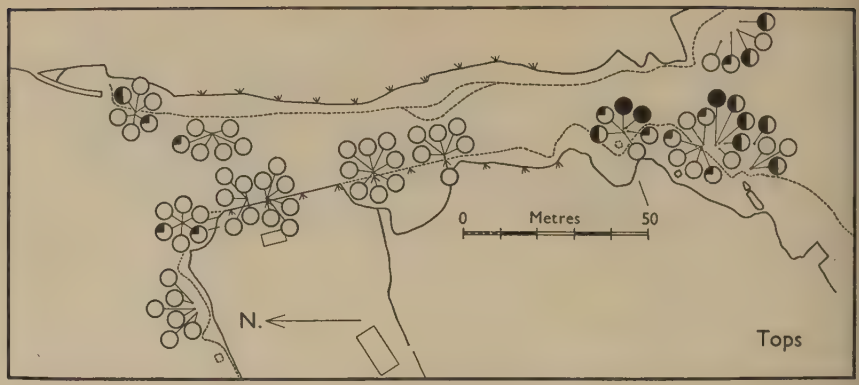


Fig. 19 (*continued*).



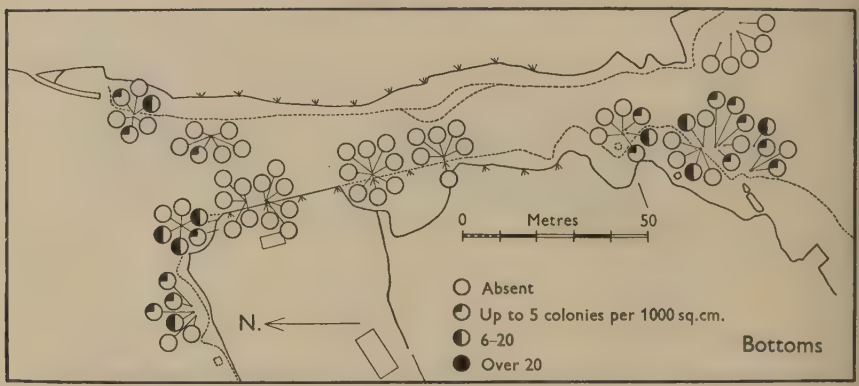


Fig. 20. Distribution of *Cellepora pumicosa* on boulders in the Lough Ine Rapids in July 1950. (Max. 43 per 1000 sq.cm., *EC*, top.)

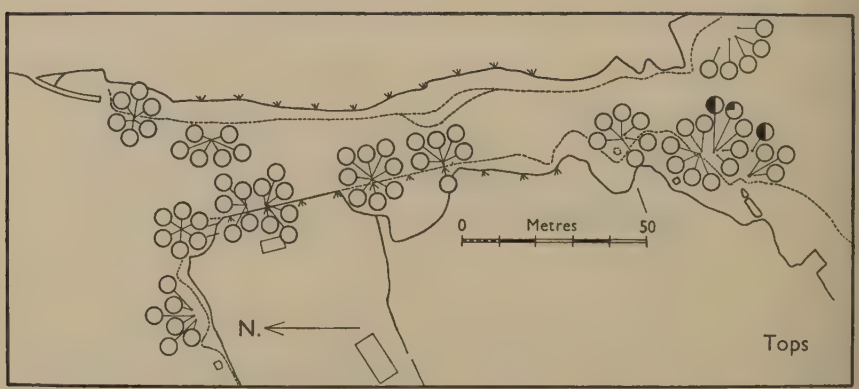


Fig. 22. Distribution of *Diastopora patina* on boulders in the Lough Ine Rapids in July 1950. (Max. 39 per 1000 sq.cm., *NR*, bottom.)

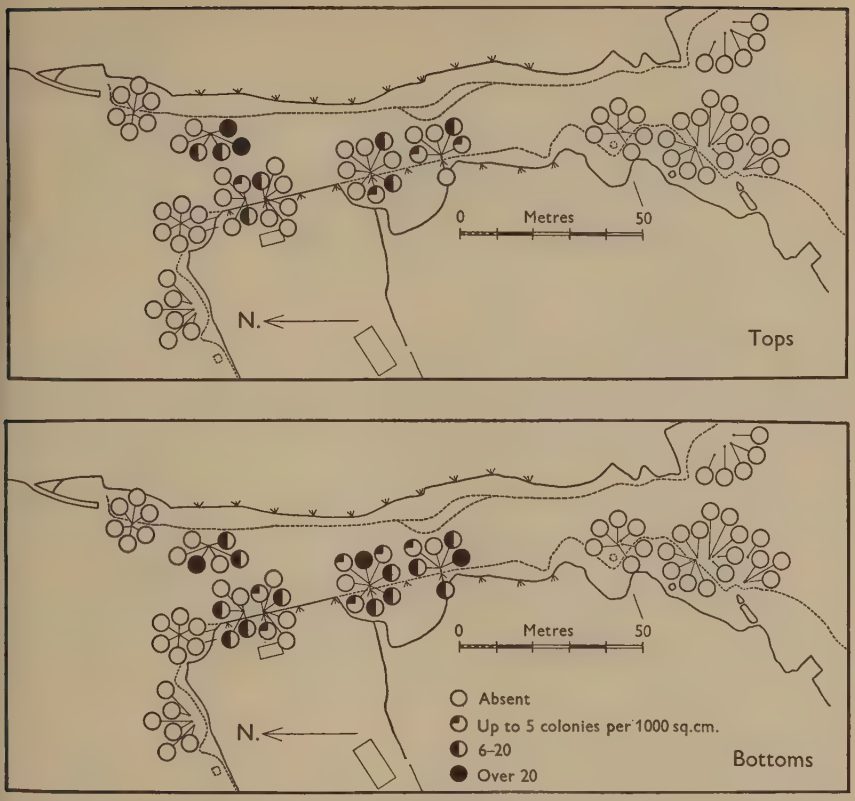


Fig. 21. Distribution of *Costazia costazii* on boulders in the Lough Ine Rapids in July 1951. (Max. 42 per 1000 sq.cm., *D1*, bottom.)

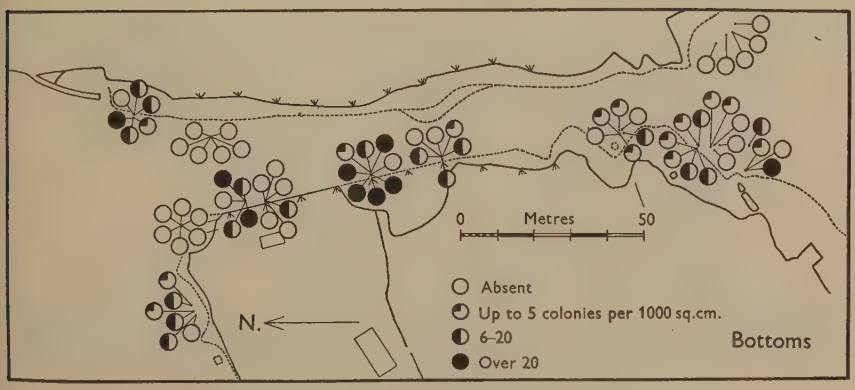


Fig. 22 (*continued*).

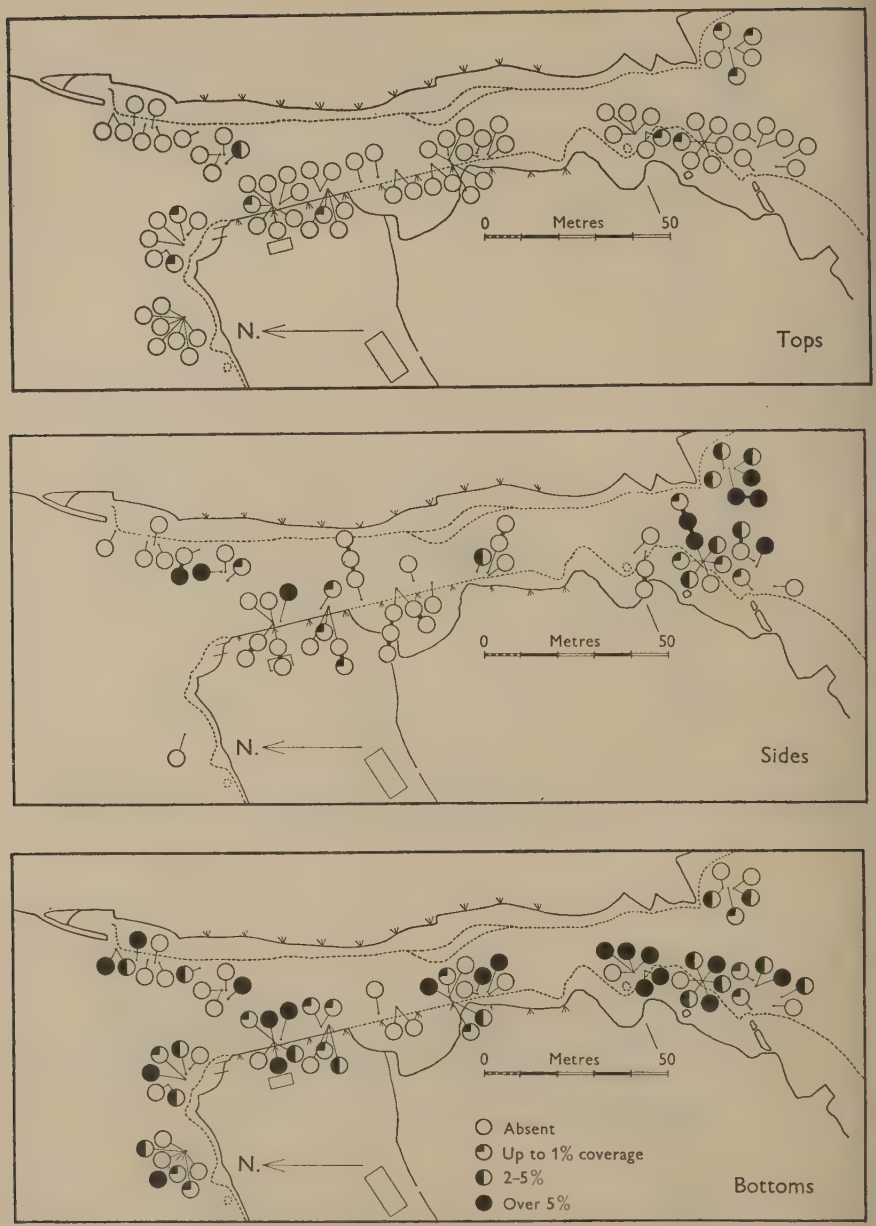


Fig. 23. Distribution of *Escharoides coccineus* on boulders in the Lough Ine Rapids in July 1948. (Max. 20%, *Sill*, bottom.)

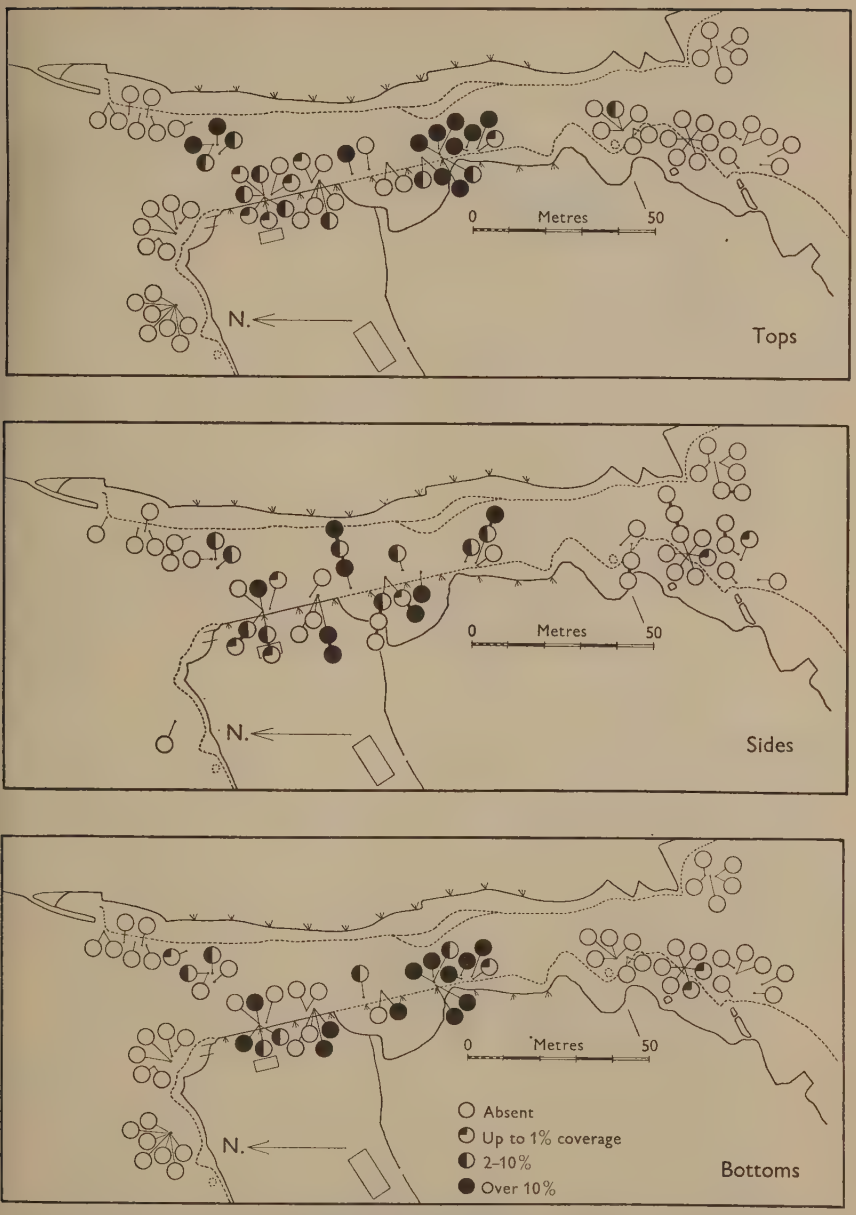


Fig. 24. Distribution of *Hippothoa hyalina* on boulders in the Lough Ine Rapids in July 1948. (Max. 85%, *Sill*, side.)

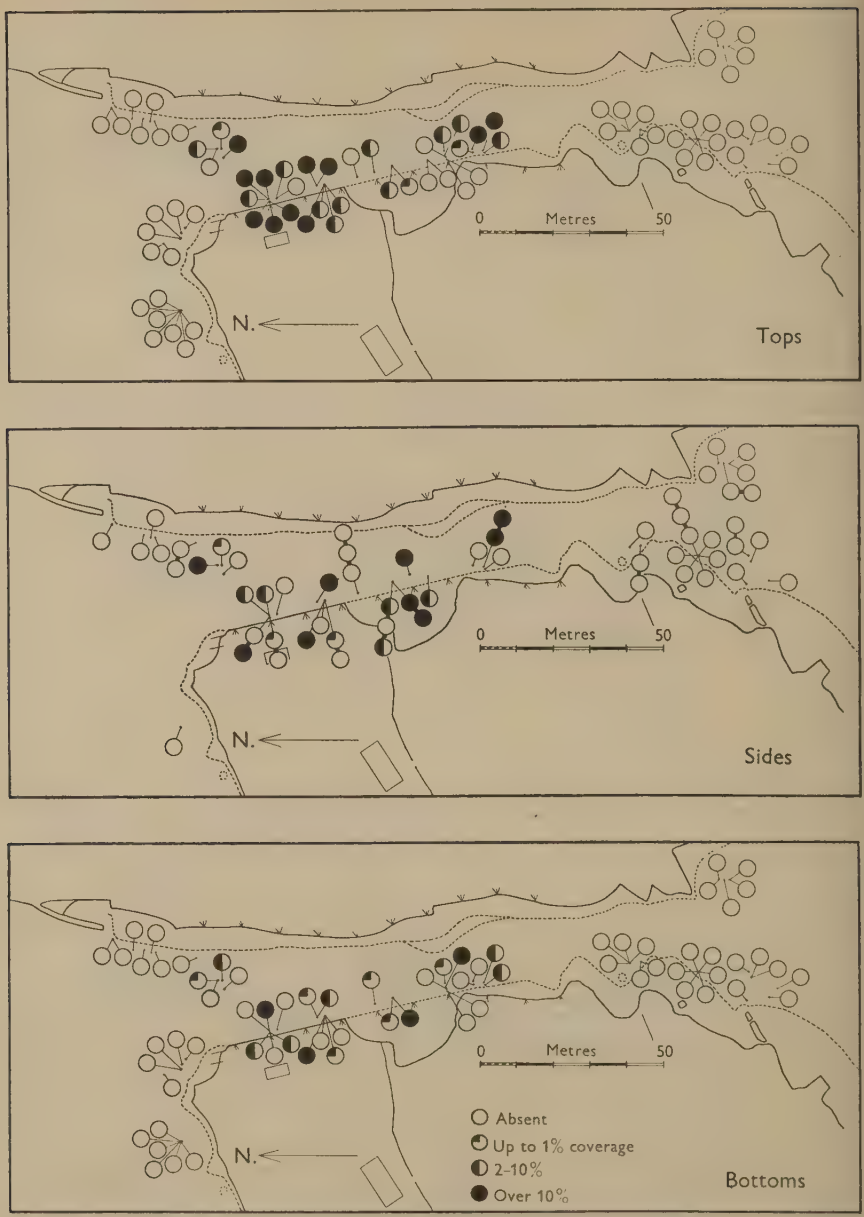


Fig. 25. Distribution of *Umbonula littoralis* on boulders in the Lough Ine Rapids in July 1948. (Max. 80%, *Sill*, side.)

Table 2. *Records of the number of boulder surfaces occupied by species occurring fairly frequently but in small quantities. July 1948.*

	Tops												Sides												Bottoms											
	CB	*RB*	*St 2*	*St 3½*	*Still*	*St 8*	*EC*	*SR*	*NR*	*P*	*D 1*	*H*	*CB*	*RB*	*St 2*	*St 3½*	*Still*	*St 8*	*EC*	*SR*	*NR*	*P*	*D 1*	*H*	*CB*	*RB*	*St 2*	*St 3½*	*Still*	*St 8*	*EC*	*SR*	*NR*	*P*	*D 1*	*H*
No. of surfaces examined	7	6	8	6	11	4	6	6	6	5	5	6	1	0	7	6	11	5	4	9	5	7	5	5	7	6	6	6	8	4	6	6	6	5	5	6
Tubularia bellis	0	0	3	5	9	2	0	0	0	0	1	0	0	·	1	2	3	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Plumularia setacea	0	0	4	0	0	0	0	0	0	0	1	0	0	·	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0
Sagartia elegans	0	0	0	1	4	0	0	0	0	0	0	0	0	·	0	0	6	2	0	0	0	0	0	0	0	0	0	0	6	4	0	0	0	0	0	0
Caryophyllia smithi	0	0	0	0	0	0	0	0	0	1	0	0	0	·	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	3	0	0
Serpula vermicularis	0	0	0	0	0	0	0	0	0	0	0	0	0	·	0	0	0	0	0	2	0	0	0	0	2	1	0	0	0	0	1	0	2	1	0	0
Balanus balanus	0	5	5	5	5	2	3	4	4	3	4	3	0	·	6	2	8	2	2	7	5	4	5	2	5	6	4	3	9	3	3	6	5	5	5	3
Uniserial Crisiidae*	1	0	0	0	0	0	1	0	0	1	1	0	0	·	0	1	1	0	0	0	0	0	0	0	0	4	1	0	1	0	0	0	0	1	0	0
Crisia eburnea	0	1	4	3	1	1	0	0	1	1	2	0	0	·	3	2	3	2	1	0	0	1	2	0	2	6	3	1	6	3	2	3	1	1	1	0
Tubulipora plumosa	2	0	3	3	2	1	3	1	0	1	4	1	0	·	1	2	4	1	0	0	0	0	0	0	2	1	3	2	7	3	1	0	0	0	4	0
Scruparia chelata	0	0	6	3	1	0	1	0	0	1	4	0	0	·	3	1	1	0	0	0	0	2	2	0	0	0	1	1	0	0	0	0	0	0	2	0
Scrupocellaria reptans	0	3	6	3	0	0	5	4	2	3	5	3	0	·	4	2	0	0	2	8	2	2	4	3	3	6	4	2	1	0	3	5	4	3	4	3
Bugula flabellata	0	1	0	0	0	0	1	0	0	0	0	0	0	·	0	0	0	0	0	2	0	2	0	0	4	5	0	0	0	0	3	0	3	2	0	2
Membraniporella nitida	0	0	0	0	0	0	0	0	0	0	0	0	0	·	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	4	1	1	2	0
Escharella variolosa	0	0	0	0	0	0	0	1	0	0	0	0	0	·	0	0	0	0	0	2	0	1	0	0	2	1	0	0	0	0	0	1	2	2	0	1
Schizomavella spp.	0	1	0	0	0	0	0	0	0	2	0	0	0	·	1	3	1	0	0	0	0	2	0	0	7	5	1	3	2	3	1	0	1	3	0	1
Cellepora pumicosa	0	0	0	0	0	0	1	0	2	1	1	0	0	·	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	1	2	2	0	1	0	1
Costazia costazii	0	0	2	3	1	0	0	0	0	1	1	0	0	·	1	0	2	0	0	0	0	0	1	0	0	0	2	1	0	0	0	0	0	0	1	0
Acanthochitona crinitus†	5	4	1	0	0	0	4	5	2	2	1	1	1	·	1	0	1	0	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0
Acmaea virginea	2	3	1	3	0	2	4	3	2	2	2	0	1	·	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0
Anomiidae	3	5	8	6	10	4	6	6	6	5	4	5	1	·	6	5	9	3	3	7	5	6	4	3	6	6	6	6	8	4	6	6	6	5	5	5
Mytilus edulis	0	0	6	6	10	4	0	0	2	0	1	0	0	·	2	3	10	3	0	0	0	0	1	0	0	0	3	3	7	4	0	0	0	0	0	0
Kellia suborbicularis	2	3	2	1	0	0	3	1	5	1	0	2	0	·	1	1	0	0	2	0	2	3	0	0	0	4	1	1	2	0	5	1	2	3	1	1
Aplidium pallidum	2	1	0	0	0	0	0	0	0	0	0	1	0	·	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0
Didemnum maculosum	1	1	3	2	0	0	0	3	3	2	2	1	0	·	1	2	1	0	3	1	1	2	1	0	1	4	5	1	0	1	4	3	3	3	3	0
Diplosoma listerianum	1	1	0	0	1	0	0	1	0	0	0	0	0	·	0	0	0	0	0	0	0	0	0	0	2	1	0	0	1	0	1	0	0	4	1	0

* Records possibly incomplete.

† See note in Fauna List.

Table 3. *Records of the number of boulder surfaces occupied by species occurring fairly frequently but in small quantities. July 1950.*

	Tops												Bottoms											
					Sill												Sill							
	CB	*RB*	*St 1½*	*St 2*	*St 5*	*St 7*	*EC*	*SR*	*NR*	*P*	*D1*	*H*	*CB*	*RB*	*St 1½*	*St 2*	*St 5*	*St 7*	*EC*	*SR*	*NR*	*P*	*D1*	*H*
No. of surfaces examined ...	6	6	5	6	8	6	6	11	4	5	6	6	6	6	5	6	8	6	6	11	4	5	6	6
Haliclona indistincta	2	1	0	0	0	0	0	1?	0	1	0	2	0	1	2	0	0	0	2	2	3	2	0	2
H. macandrewii	2	1	1	0	0	0	0	0	3	0	0	2	1	4	2	0	1	0	4	2	5	1	0	1
H. limbata	0	0	0	0	0	1	3	1	1	0	0	0	3	1	2	2	1	0	2	3	4	2	0	2
Adocia cinerea	2	0	0	0	0	0	3	5	1	0	0	1	1	1	1	0	0	0	3	4	3	0	0	1
Mycale rotalis	1	1	0	0	0	0	3	1	2	1	1	2	0	0	1	0	0	0	1	3	2	2	1	4
M. macilenta	0	0	1?	1	1	0	0	0	2	0	0	0	0	0	0	3	1	1	0	0	0	1	1	0
Myxilla rosacea	2	4	1	2	2	0	3	4	1	1	2	3	5	4	3	4	1	0	2	1	0	2	2	2
Hymedesmia pansa	0	0	0	0	0	0	0	0	0	0	1	0	2	0	1	0	2	0	0	0	0	1	0	2
Hymeniacidon perlevis	0	1	0	0	0	0	0	1	1	0	0	1	0	2	0	0	0	0	1	0	0	0	0	0
Dysidea fragilis	0	0	0	0	0	0	1	1	1	1	1	2	4	5	0	0	1	1	2	4	3	3	0	3
Plumularia setacea	0	0	0	3	1	2	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Caryophyllia smithi	1	0	0	0	0	0	0	0	0	0	0	2	1	0	1	0	0	0	0	1	0	1	0	1
Spirorbis spp.	1	0	0	0	2	0	0	3	1	4	2	0	5	6	·	2	6	3	6	11	4	5	5	5
Uniserial Crisiidae	0	3	0	0	0	0	0	1	0	0	0	1	0	5	0	2	1	0	0	0	0	0	1	3
Crisia eburnea	0	1	4	2	4	3	0	3	0	0	3	0	5	4	4	6	4	4	0	0	0	0	4	4
Lichenopora hispida	0	0	0	0	0	0	0	0	0	0	0	0	6	0	1	1	0	1	1	3	1	0	0	5
Acanthochitona crinitus	3	0	0	0	0	0	1	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Diodora apertura	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1	0	1	0	1	5	1	0	0	1
Acmaea virginea	3	1	0	1	0	0	1	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monia squama	2	0	2	1	0	0	4	3	4	0	2	1	1	0	3	1	4	4	2	1	3	0	4	2
Kellia suborbicularis	0	0	0	1	0	0	1	0	1	0	0	0	0	3	2	0	2	0	1	0	2	0	0	0

FAUNA LIST (SEDENTARY SPECIES)

The numbers after each station are the numbers of boulder surfaces on which a species was found. Records for the year stated are complete except for Porifera collected in 1948.

PORIFERA

Leucosolenia coriacea (Montagu) 1948: present. 1950: tops, none: bottoms, *CB* 2; *RB* 1; *St* 1½ 1.
L. contorta Bowerbank 1950: tops, *St 5* 1: bottoms, *CB* 1.
L. complicata (Montagu) 1950: tops, *D1* 1: bottoms, none.
L. botryoides (Ellis & Solander) 1948: present.
Sycon ciliatum (Fabricius) 1948: present. 1950: tops, none: bottoms, *CB* 1; *St 5* 1; *H* 1.
Leuconia nivea (Grant) 1948: present. 1950: tops, none: bottoms, *CB* 2; *RB* 1; *St* 1½ 1; *St 2* 2; *EC* 4; *SR* 9; *NR* 4; *D1* 3.
L. johnstonii Carter 1950: tops, none: bottoms, *St* 1½ 2; *EC* 1; *NR* 2.
Plakina monolopha Schulze 1948: present. 1950: tops, none: bottoms, *CB* 4; *RB* 1.
Oscarella lobularis (Schmidt) 1948: present. 1950: tops, *SR* 1; *NR* 1; *D1* 1: bottoms, *CB* 1; *St* 1½ 1; *SR* 3; *NR* 1; *P* 1; *D1* 2; *H* 1.
Stelletta lactea (Carter) 1950: tops, none: bottoms, *RB* 1; *St* 1½ 2.
Pachymatisma johnstonia (Bowerbank) 1948: present. 1950: tops, none: bottoms, *RB* 1.
Suberites ficus (Linnaeus) 1948: present.
S. carnosus (Johnston) 1950: tops, none: bottoms, *SR* 1; *D1* 1.
Pseudosuberites sulphureus (Bean) 1950: tops, none: bottoms, *EC* 1.
Haliclona indistincta (Bowerbank) 1948: present. 1950: Table 3.
H. macandrewii (Bowerbank) 1948: present. 1950: Table 3.
H. rosea (Bowerbank) 1950: tops, none: bottoms, *SR* 1; *NR* 1; *P* 1.
H. limbata (Montagu) 1948: present. 1950: Table 3.
H. cancellata (Sowerby) 1950: tops, none: bottoms, *D1* 1; *H* 1.
H. angulata (Bowerbank) 1950: tops, *CB* 1: bottoms, *CB* 2; *RB* 1; *St* 1½ 1; *H* 2.
H. condensa (Bowerbank) 1948: present.
Adocia cinerea (Grant) 1948: present. 1950: Table 3.
**Mycale rotalis* (Bowerbank) 1948: present. 1950: Table 3.
**M. contarenii* (Martens) 1948: present.
M. macilenta (Bowerbank) 1948: present. 1950: Table 3.
M. minima (Waller) 1948: present.
Amphilectus fucorum (Esper) 1948: present. 1950: Fig. 4.
Hemimycale columella (Bowerbank) 1948: present.
Myxilla rosacea (Lieberkuhn) 1948: present. 1950: Table 3.
M. incrustans (Johnston) 1948: present. 1950: tops, none: bottoms, *St 5* 1.
M. perspinosa Lundbeck 1950: tops, none: bottoms, *St 2* 1.
Lissodendoryx diversichela Lundbeck 1950: tops, none: bottoms, *NR* 1.
Phorbas fictitius (Bowerbank) 1948: present. 1950: tops, none: bottoms, *CB* 1.
Hymedesmia bronstedi Burton 1948: present. 1950: Fig. 5.
H. pansa Bowerbank 1950: Table 3.
H. paupertas Bowerbank 1950: tops, none: bottoms, *CB* 1.
H. zetlandica Bowerbank 1950: tops, *St 2* 1; *St 5* 1: bottoms, *SR* 1.
H. longistyles Lundbeck 1948: present.
H. similis Lundbeck 1948: present.
H. nummulus Lundbeck 1950: tops, none: bottoms, *SR* 1.
H. procumbens Lundbeck 1950: tops, none: bottoms, *RB* 1.
H. lieberkühni Burton 1948: present.
Spanioplon armaturum (Bowerbank) 1950: tops, *NR* 1: bottoms, *CB* 1; *St* 1½ 1; *SR* 1.
Menyllus nigricans (Bowerbank) 1950: tops, none: bottoms, *St 7* 2.
M. ingalli (Bowerbank) 1950: tops, *RB* 1; *D1* 1: bottoms, *RB* 2; *D1* 1.

* Dr Burton has written to us about *Mycale rotalis* and *M. contarenii* as follows: 'it is not impossible that these two may be forms of a single species. Certainly there is no evidence of difference in habitat and they can readily replace each other'. It seems possible that the same may be true of species in other genera of Porifera.

Stylostichon plumosus (Montagu) 1950: tops, none: bottoms, *St 5* 1; *D1* 1.
S. bihamigera (Waller) 1948: present. 1950: tops, none: bottoms, *NR* 1.
Plocamionida ambigua (Bowerbank) 1950: tops, none: bottoms, *CB* 1; *RB* 1; *St 1½* 1; *SR* 1.
Plocamilla coriacea (Bowerbank) 1948: present. 1950: tops, *H* 1: bottoms, *CB* 1; *St 1½* 1; *SR* 2.
Microciona atrosanguinea Bowerbank 1948: present. 1950: tops, *D1* 1: bottoms, *SR* 1.
M. microchela (Stephens) 1948: present. 1950: tops, none: bottoms, *St 2* 1.
M. acanthotoxa (Stephens) 1948: present. 1950: tops, *St 1½* 1: bottoms, *St 1½* 1; *D1* 1.
Ophlitaspongia seriata Bowerbank 1948: present. 1950: tops, none: bottoms, *St 5* 2.
Halichondria bowerbanki Burton 1948: present. 1950: Fig. 6.
H. panicea (Pallas) 1948: one record.
Hymeniacidon perlevis (Montagu) 1948: present. 1950: Table 3.
Ulosa tupha (Pallas) 1950: tops, *St 2* 1: bottoms, *St 7* 1.
Halisarca dujardinii Johnston 1948: present. 1950: tops, *D1* 1: bottoms, none.
Aplysilla sulphurea Schulze 1950: tops, none: bottoms, (? *RB* 1); *P* 1.
A. rosea (Barrois) 1948: present.
Spongionella carteri (Burton) 1950: tops, *CB* 1: bottoms, *EC* 1.
Dysidea fragilis (Montagu) 1950: Table 3.

HYDROZOA

Syncoryne eximia (Allman) 1948: tops, Sill 2; *St 8* 1: sides, none: bottoms, none. 1950: tops, *SR* 1: bottoms, none.
Eudendrium rameum (Pallas) 1948: tops, none: sides, none: bottoms, *RB* 1.
Tubularia bellis Allman 1948: Table 2.
Halecium halecinum (L.) 1948: tops, none: sides, none: bottoms, *D1* 1.
Sertularella polyzonias (L.) 1948: tops, *St 2* 1: sides, none: bottoms, none.
Sertularia operculata L. 1948: Fig. 7.
Plumularia setacea (Ellis & Solander) 1948: Table 2. 1950: Table 3.

SCYPHOZOA

Aurelia aurita (L.) Scyphistoma stage. 1948: tops, none: sides, none: bottoms, *NR* 1.

ANTHOZOA

Parerythropodium hibernicum Renouf 1948: tops, none: sides, none: bottoms, *RB* 4. 1950: tops, none: bottoms, *RB* 4; *H* 2.
Tealia felina (Linnaeus) 1948: tops, *RB* 1; *NR* 1; *D1* 1: sides, *D1* 1: bottoms, *D1* 1.
Anthopleura ballii (Cocks) 1948: Fig. 8.
Metridium senile (Linnaeus) 1948: Fig. 9.
Sagartia elegans (Dalyell) 1948: Table 2. 1950: tops, *St 5* 1; *D1* 1: bottoms, *St 5* 2.
Actinothoe anguicoma (Price) 1948: tops, none: sides, none: bottoms, *H* 1.
Caryophyllia smithi Stokes 1948: Table 2. 1950: Table 3.
Corynactis viridis Allman 1948: Fig. 10.

POLYCHAETA

Serpula vermicularis Linn. 1948: Table 2. 1950: tops, none: bottoms, *RB* 1; *EC* 4.
Hydroides norvegica (Gunnerus) 1948: tops, *St 8* 1; *D1* 1: sides, none: bottoms, none.
Pomatoceros triqueter Linn. 1948: Fig. 11.
Spirorbis spp. 1948: Fig. 12. 1950: Table 3. The records for the following species of *Spirorbis* were obtained by examination of samples from the material collected, and therefore are not necessarily complete.
S. corrugatus (Montagu) 1950: tops, *CB, SR, NR, P*: bottoms, *CB, St 2, St 5, St 7, EC, SR, NR, P, D1, H.*
S. pagenstecheri Quatrefages 1950: tops, *P*: bottoms, *CB, RB, NR, P, H.*
S. borealis Daudin 1950: tops, *CB, St 5, SR, NR, P, D1*: bottoms, *CB, RB, St 2, St 5, St 7, EC, SR, NR, P, D1, H.*
S. mediterraneus Caullery & Mesnil 1950: tops, *CB, H*: bottoms, *CB, RB, St 5, St 7, EC, SR, NR, P, D1, H.*
S. granulatus (Linn.) 1950: tops, *St 2, St 5*: bottoms, *CB, RB, St 2, St 5, St 7, EC, SR, NR, P, D1, H.*

IRRIPEDIA

Verruca stroemia (O. F. Müller) 1948: Fig. 13.
Chthamalus stellatus (Poli) 1948: tops, *Sill* 2: sides, *Sill* 2: bottoms, none.
Balanus balanus (Linn.) 1948: Table 2.
B. crenatus Bruguière 1948: Fig. 14.

OLYZOA

Pedicellina cernua (Pall.) 1948: tops, *P* 1: sides, none: bottoms, none.
Crisidia cornuta (Linn.)
Filicrisia geniculata (M.-E.)
These two species were not separated in the field, and are included in Table 2 (1948) and Table 3 (1950) as 'Uniserial Crisiidae'. Definite records are: *Crisidia cornuta* 1948: sides, *Sill* 1. *Filicrisia geniculata*, Sept. 1946: bottoms, *St 9* 1.
Crisia eburnea (Linn.) 1948: Table 2. 1950: Table 3.
Tubulipora plumosa W. Thomps. 1948: Table 2.
Diastopora patina (Lamk.) 1950: Fig. 22.
Lichenopora hispida (Flem.) 1950: Table 3.
Aetea sica (Couch) 1948: tops, none: sides, none: bottoms, *CB* 1.
A. truncata (Landsbr.) 1948: tops, *CB* 1: sides, none: bottoms, none.
Scruparia chelata (Linn.) 1948: Table 2.
Callopora lineata (Linn.) 1948: tops, none: sides, none: bottoms, *St* 3½ 1.
C. dumerilii (Aud.) 1948: tops, none: sides, none: bottoms, *CB* 1.
Caberea boryi Aud. 1948: tops, none: sides, none: bottoms, *CB* 1; *P* 1.
Scrupocellaria scruposa (Linn.) 1948: tops, none: sides, *P* 1: bottoms, *EC* 1; *P* 1. 1950: tops, none: bottoms, *CB* 3; *SR* 1; *P* 1.
S. scrupea Bsk. 1948: tops, *CB* 2; *St* 3½ 1; sides, none: bottoms, *RB* 1. 1950: tops, *RB* 3; *SR* 1: bottoms, *CB* 1; *RB* 2.
S. reptans (Linn.) 1948: Table 2. 1950: Fig. 19.
Bugula flabellata (Thomps.) 1948: Table 2.
Membraniporella nitida (Johnst.) 1948: Table 2.
Hippothoa distans MacG. 1948: tops, none: sides, none: bottoms, *CB* 1.
H. hyalina (Linn.) 1948: Fig. 24.
Haplopoma impressum (Aud.) 1948: tops, none: sides, *St* 3½ 1: bottoms, *Sill* 2.
Escharella variolosa (Johnst.) 1948: Table 2.
Escharoides coccineus (Abild.) 1948: Fig. 23.
Schizoporella unicornis (Johnst.) 1948: tops, none: sides, *SR* 1: bottoms, *P* 2.
Schizomavella auriculata (Hass.)
S. linearis (Hass.)
These two species have not been separated in the field, and are included in Table 2 (1948) as *Schizomavella* spp. Definite records are: *S. auriculata* 1950: tops, *RB* 1: bottoms, *CB* 2; *RB* 1; *EC* 1. *S. linearis* 1950: bottoms, *CB* 2; *RB* 4.
Cryptosula pallasiana (Moll.) 1948: tops, *St* 3½ 1; *St 8* 1; *EC* 1; *P* 1: sides, none: bottoms, none.
Microporella ciliata (Pall.) 1948: tops, none: sides, *Sill* 1: bottoms, *CB* 1; *St* 3½ 1; *Sill* 2; *D1* 1.
Fenestrulina malusii (Aud.) 1948: tops, none: sides, none: bottoms, *D1* 1.
Smittina landsborovii (Johnst.) 1948: tops, none: sides, *P* 1: bottoms, *SR* 3; *P* 2.
Umbonula littoralis Hastings 1948: Fig. 25.
U. ovicellata Hastings 1948: tops, *RB* 2; *St* 3½ 1: sides, none: bottoms, none.
Cellepora armata Hcks. 1948: tops, none: sides, none: bottoms, *CB* 1. 1950: tops, none: bottoms, *CB* 2; *P* 1.
C. pumicosa (Linn., Bsk. emend.) 1948: Table 2. 1950: Fig. 20.
Costazia costazii (Aud.) 1948: Table 2. 1950: Fig. 21.
Amathia lendigera Linn. 1948: tops, none: sides, none: bottoms, *CB* 1; *H* 1.

PLACOPHORA

Tonicella rubra (Linn.) 1950: tops, *CB* 1; *SR* 1: bottoms, none.
Acanthochitona crinitus (Pennant) 1950: Table 3. In 1948 (Table 2) this species and *Tonicella rubra* were not separated.

GASTROPODA

Emarginula fissura (Linn.) 1948: tops, *RB* 1: sides, none: bottoms, *RB* 1; *EC* 1. 1950: tops none: bottoms, *P* 1; *D1* 1.
Diodora apertura (Montagu) 1948: tops, *EC* 1; *NR* 1; *D1* 1: sides, none: bottoms, *EC* 3 1950: Table 3.
Patella vulgata Linn. 1949: *Sill.*
P. aspera Roding 1949: *Sill.*
Acmaea virginea (Müller) 1948: Table 2. 1950: Table 3.

PELECYPODA

Monia squama (Gmelin) 1950: Table 3.
Heteranomia squamula (Linn.) 1950: Fig. 18. In 1948 (Table 2) this species and *Monia squama* were not separated.
Mytilus edulis Linn. 1948: Table 2. 1950: Fig. 17.
Modiolus barbatus (Linn.) 1948: occasional specimens on *Sill*, but records incomplete 1950: none.
M. phaseolinus (Philippi) 1948: tops, *CB* 1: sides, none: bottoms, none. 1950: tops, *EC* 1 *D1* 1: bottoms, *St 1½* 2; *St 5* 1.
Musculus discors (Linn.) 1948: tops, *SR* 1; *P* 1; *D1* 1: sides, none: bottoms, none.
M. marmoratus (Forbes) 1948: Fig. 16.
Kellia suborbicularis (Montagu) 1948: Table 2. 1950: Table 3.
Hiatella arctica (Linn.) 1948: Fig. 15.

TUNICATA

Morchellium argus (Milne Edwards) 1948: tops, *EC* 1; *NR* 2; *P* 1: sides, *P* 1: bottoms, *P* 2 *D1* 1.
Aplidium pallidum (Verrill) 1948: Table 2.
A. (*Amaroucium*) sp. 1948: tops, *St 3½* 1: sides, none: bottoms, *RB* 1.
Sidnyum turbinatum (Savigny) 1948: tops, *H* 1 ?: sides, *St 8* 1; *P* 1 ?.
Tridemnum tenerum (Verrill) 1948: tops, none: sides, none: bottoms, *St 3½* 1.
Didemnum maculosum (Milne Edwards) 1948: Table 2. This species includes *Leptoclinum maculosum*, *L. durum*, and *L. fulgens* given by Alder & Hancock (1911); all three of these varieties were found, with no obvious differences in distribution, although *L. durum* was less plentiful than the other two.
Unidentified Didemnidae 1948: tops, *St 3½* 1; *D1* 1: sides, *St 3½* 3; *EC* 1: bottoms, *RB* 7 *St 3½* 1; *NR* 6; *P* 3; *H* 1.
Diplosoma listerianum (Milne Edwards) 1948: Table 2.
Ascidia mentula Müller 1948: tops, *CB* 1: sides, *P* 1 ?: bottoms, *CB* 3; *EC* 2; *NR* 1; *P* 1.
A. conchilega Müller 1948: tops, none: sides, none: bottoms, *P* 1+1 ?.
Polycarpa sp. 1948: tops, *RB* 1: sides, none: bottoms, none.
Botryllus schlosseri (Pallas) 1948: tops, *St* 2 1; *St 3½* 1; *St 8* 1: sides, none: bottoms, *St 2* 1.
Botrylloides leachi (Savigny) 1948: tops, *St 8* 1; *P* 1: sides, none: bottoms, *RB* 1; *St 8* 1 *H* 1.
Pyura microcosmus (Savigny) 1948: tops, none: sides, none: bottoms, *EC* 1; *P* 1.

A DISEASE OF MANX SHEARWATERS: FURTHER OBSERVATIONS IN THE FIELD

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(With 2 Figures in the Text)

INTRODUCTION

n 1946 an epizootic disease was found to be occurring among the juvenile Manx hearwaters (*Puffinus puffinus*) on Skomer Island, Pembrokeshire. A similar outbreak ollowed in 1947, and this was investigated by Dane (1948*a*, *b*). From material sent o Cambridge Miles & Stoker (1948) isolated a virus which appeared to be the causal gent and they suggested that the disease be named puffinosis. Further work on the irus is being published by Stoker and Miles (in the press).

Epizootics in wild animal populations have not often been studied because of the bvious difficulties involved. However, in the case of the puffinosis epizootics there vere certain features which made a detailed investigation possible. In the first place Manx shearwaters could be caught and examined fairly easily, and much had already been discovered about their life history and habits by Lockley (1942) and others; econdly, Skomer was an ideal place for such an investigation as it is isolated and of convenient size; and finally planning was simplified by the regularity with which the pizootics occurred. Because of these rather exceptional advantages we decided to ontinue investigations on a larger scale in 1948 and 1949. In 1950 and 1952 we visited he island again, but on these occasions only to make certain limited observations. Before continuing with an account of our work in these years it will be necessary to give brief description of Skomer, the Manx shearwater, and the epizootics of 1946 and 947.

Skomer lies about one mile off the coast of southern Pembrokeshire. It is a rocky, vind-swept island with steep cliffs, well known as a breeding ground for many species f sea-bird. There are few trees or shrubs on the island, but rocky outcrops and stone valls are plentiful. The walls date from the time when about one-third of the island vas under cultivation; recently, although the island has been inhabited at most times, ttle cultivation has been attempted. For convenience when investigating the uffinosis epizootics we divided up the island into the areas shown on the map (Fig. 1).

Adult Manx shearwaters begin visiting Skomer to breed in February and March fter having spent the winter at sea. On land they are strictly nocturnal and all visits re made after dark when the danger from gulls and other predators is slight. In May† ne egg is laid at the end of a nesting burrow. Though shearwaters nest in almost very part of the island the density of population varies greatly. Some of the most

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† On Skokholm in 1952 Mr G. V. T. Matthews (personal communication) estimated that the ajority of eggs were laid during the second and third weeks of May.

crowded colonies are on the slopes above the cliffs and along the walls. The incubation period lasts for a little over 50 days. For a week the young chick is brooded; then it is left alone during the daytime and visited only at night to be fed. When about 60 days old the chick is deserted by the parents, who leave the island not to return until the following spring. For the next 10–15 days the young shearwater remains in its burrow unfed, but maturing. Then it makes its way to the sea and like its parents will not visit the island again that year. At the beginning of its fast the young bird is fat, weighing more than an adult; and its new feathers are hidden beneath a mass of down. By the time it is ready to leave the island it has changed considerably; much of the fat has been used up and only a few traces of down remain. The amount of down present on

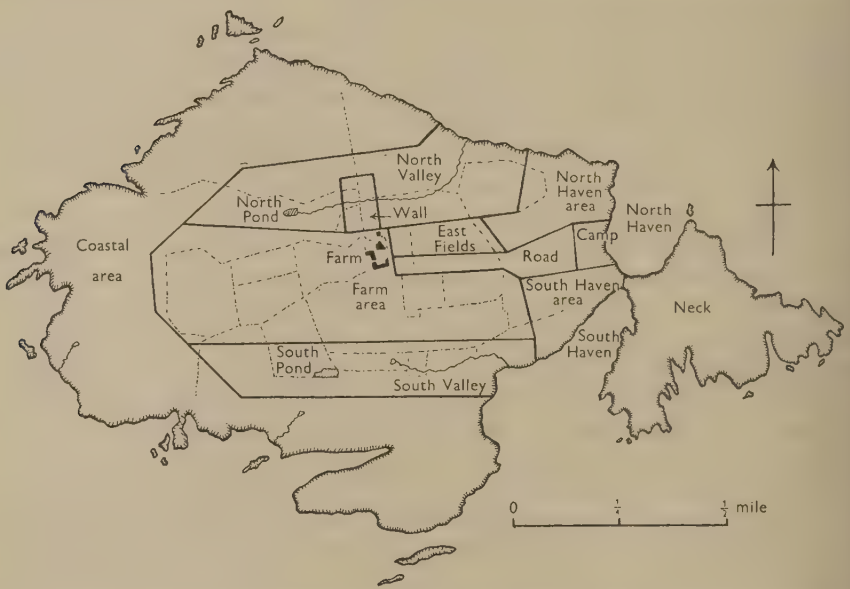

Fig. 1. Skomer Island showing the stone walls (broken lines) and the areas (full lines) into which the island was divided for the purpose of the investigation.

a juvenile shearwater is a useful, though approximate guide to its age. For the first few nights after desertion the young bird stays below ground, then it begins a series of nightly excursions into the outside world. At first these do not take it far from its burrow, but later, as the time approaches for the journey to the sea, it may wander 100 yards or more before returning home. When it is outside at night the young shearwater takes the opportunity of exercising its wings. If there is a suitable rock or stone nearby it will clamber on to this to do its wing-flapping, and if such perches are scarce several young birds may visit the same one. For birds reared near the cliffs the journey to the sea is short and probably they leave when a few days younger than their fellows from the colonies in the centre of the island. These birds from the centre of the island may have half a mile of difficult ground over which to run and flap and scramble before reaching the sea, for they are not yet able to fly. Estimates of the total number

of adult Manx shearwaters breeding on Skomer vary, but there are probably over 50,000 birds.

In 1946 and 1947 puffinosis epizootics occurred on Skomer starting about the beginning of September, most of the cases being recorded in North Valley (Fig. 1). The disease, which only affected juveniles, was characterized by blisters on the webs of the feet and sometimes also by conjunctivitis. The case fatality rate was high, and the morbidity rate varied with the locality, sometimes about half the local population being infected.

The vast majority of birds found with signs of the disease were between 70 and 75 days old (i.e. 10–15 days after desertion by their parents). It was thought that the infection was passed indirectly from bird to bird by contamination of soil and stones with virus from burst blisters. The original source of infection was not discovered.

THE 1948 AND 1949 EPIZOOTICS

During the 1948 season we were able to make two visits to the island: from 23 August to 4 September and later from 13 to 17 September. In 1947 the disease had first been noticed in North Valley and along the Wall (Fig. 1), and the course of the epizootic was followed only in these areas. Few observations were made elsewhere and the extent to which the disease occurred in other parts of the island was not properly known, though it was thought to be less prevalent. In 1948 our main attention was again paid to North Valley and the Wall, although limited observations were also made in the Farm area, along the Road, in the North Haven area and around our Camp. On each night during our time on the island birds were examined in North Valley and along the Wall, and normally also in the Road and Camp areas. All birds were ringed with numbered aluminium rings on the first occasion that they were seen. No evidence of puffinosis was found until 29 August, when three juveniles with inflamed webs were found along the Wall. Next day two juveniles with blisters were found in the same area, and on the following day there were two more. On 1 September nine birds with blistered feet, four of which had died, were picked up in North Valley and in the Wall area. From then on numerous diseased birds were present and by the time we left on 4 September it was clear that a very intense epizootic might be expected. Unfortunately, it was not possible for an observer to be on the island throughout the first half of September, and the next visit was from 13 to 17 September. At this time the epizootic was in full swing and over 75% of the birds picked up in North Valley and the Wall area were infected (Table 1). The other areas were not examined in detail, but along the Road no infected birds were found. When we examined birds in this area we did so before visiting the heavily infected areas to minimize the risk of spreading the disease ourselves. A small number of shearwaters were examined in the Farm area, the North Haven area and in the Camp area; they showed an infection rate of 30–40%, or about half that found in North Valley and along the Wall. Numerous juvenile shearwaters were still leaving their burrows when we finally left the island on 17 September and there was then no sign of the epizootic abating.

In 1949 we were present on the island from 27 August until 16 September. Our experience of the disease in 1947 and 1948 had led us to expect that we should be early enough again to observe the beginning of the epizootic, but on the first night six

of twenty-five juveniles picked up in North Valley and along the Wall were found to be blistered, and on all succeeding nights blistered birds were found. Table 2 shows the course of the epizootic in these areas. From these figures it seems fairly clear that the epizootic had not reached its peak at the time of our arrival and that it reached a stable intensity on 30–31 August, about which level it fluctuated throughout the rest of our period of observation without showing any clear-cut evidence of increase or decrease.

Table 1. *Infection-rate among juvenile shearwaters in different areas of Skomer in 1948 (13–17 September) and 1949 (27 August–16 September)*

	Birds examined						Birds infected when first seen 1949	
	1948			1949				
	Total	Infected	%	Total	Infected	%	Number	%
Coastal area	—	—	—	66	2	3	2	3
Farm area	17	6	35	133	29	22	28	21
North Valley	135	102	76	485	178	37	122	25
Wall	38	30	79	146	67	46	47	32
South Valley	—	—	—	96	22	23	22	23
East Fields	—	—	—	25	2	8	2	8
Road	25	0	0	116	2	2	1	1
S. Haven area	—	—	—	12	0	0	0	0
N. Haven area	19	6	32	95	5	5	5	5
Camp	8	3	37	66	2	3	0	0
Neck	—	—	—	73	0	0	0	0

Comparison with the early course of the epizootic in 1947 and 1948 leads us to suggest that the first cases probably occurred about 24 August. This was about a week earlier than the previous three epizootics had started. Possibly there was an earlier breeding season in 1949, and this factor indirectly influenced the time of onset of the epizootic. We visited North Valley and the Wall each night, but we also examined enough birds in all other parts of the island to estimate the various local rates of infection.

Despite the early start of the epizootic in 1949 it did not reach an intensity approaching that found in 1948 in North Valley and in the Wall area. The total number of birds examined was much greater in 1949 than in 1948, but the number seen in North Valley and by the Wall was large enough in both years for comparisons to be made. A significantly higher percentage of birds was infected in 1948, and the rate of infection was almost the same in both areas, but in 1949 there were more infected birds by the Wall than in North Valley. Table 1 shows the percentage infection-rate for the different areas in 1948 and 1949, but the figures for the two years are not quite comparable because the investigations were not over identical periods. Table 1 also shows the percentage of birds in the different areas found to be infected when first picked up in 1949. These figures are given because in most areas only one or a few visits were paid, and had the examination of other areas been as intense as that in North Valley and along the Wall the percentage of infected birds would have been raised by the demonstration of the development of blisters in birds which were healthy when first seen. Therefore, the figures given in the last two columns enable the infection-rate in different areas to be compared fairly accurately.

The weather varied in the two years. 1948 was a wet season in which the growth of

bracken on the island was prodigious. 1949 was a dry season and vegetation in general was not nearly so rank. That this may have been significant in determining the different intensity of the epizootics in the two years may be judged from a comparison of the rates of infection in relation to the vegetation of the various areas. The Coastal area is very open country with thrift dominant and some heather away from the cliffs. The concentration of breeding shearwaters in this area was low and the young birds appeared to leave earlier than those from the inland nesting burrows. Only two infected birds were found in this area: one, a very downy juvenile sitting at the mouth of its burrow, must have become infected in the area; the other bird was older and might have been passing through on its way to the coast from inland. The North and South Haven areas are more sheltered and have a much heavier bracken covering.

Table 2. *Number of birds picked up in North Valley and by the Wall and the percentage found infected in 1949*

	Total	Infected	% infected
27 Aug.	25	6	24
28 Aug.	52	9	17
29 Aug.	46	7	15
30 Aug.	59	18	30
31 Aug.	71	35	49
1 Sept.	68	24	35
2 Sept.	44	22	50
3 Sept.	53	20	38
4 Sept.	61	25	41
5 Sept.	62	26	41
6 Sept.	59	28	47
7 Sept.	61	29	47
8 Sept.	40	11	28
9 Sept.	46	22	48
15 Sept.	61	17	28

Infection does not seem to be very common in these areas, although the figures for nineteen birds in 1948 led us to expect more numerous infected birds than we found in 1949. The Neck is mainly open country like the Coastal area but it also has parts which are thickly covered with bracken. The density of breeding birds was smaller than on the main part of the island. No infected birds were noted among the seventy-three examined here. The Road area is a narrow strip on either side of the road from our camp to the farm. It is fairly open with small areas of low bracken and numerous rocks. There is a stone wall along its southern boundary from the farm half way to the camp. Numerous birds breed in this area, but the incidence of the disease is as low as that in the coastal areas. The Camp area is similar to the North and South Haven areas but is considered separately because several infected birds were kept in cages near the camp. Despite this in both 1948 and 1949 the rate of infection did not differ substantially from that in the adjoining North Haven area. The Farm area and the East Fields are the main areas which have been in cultivation in recent years; they are fairly open although parts are becoming overgrown with bracken. The highest concentration of breeding birds in both areas is along those walls bordering the uncultivated areas, particularly where the Farm area adjoins South Valley and where the East Fields adjoin North Valley. The number of birds picked up in the East Fields was not large and the amount of disease was surprisingly low considering the proximity of North

Valley where the infection-rate was so high. However, the infection-rate in the Farm area was not substantially different from that in South Valley. North and South Valleys are very similar; both contain streams, the upper parts of which are usually dry in September, but which contain small pools towards the sea. Cover is fairly dense along the valleys although both show a number of clearings. The reeds in the upper parts and the bracken elsewhere are denser in North Valley, while the brambles near the cliffs are more abundant in South Valley. The Wall area has the densest vegetation of all. Most of this area is covered with tall bracken, but by the stream there are thick clumps of reeds. Two old walls running through this area are almost the only clear patches. In 1949 the infection rate in North and South Valleys was not significantly different, but the Wall area showed a higher percentage of diseased birds than anywhere else. On the neighbouring island of Skokholm where shearwaters also breed, several hundred birds were examined with the help of Mr Peter Conder and Miss J. Keighley, and more than a dozen scattered cases were found. The breeding colonies on Skokholm are chiefly on ground which resembles in character the Coastal area of Skomer, and the rate of infection was found to be similar in these two areas.

THE COURSE OF THE DISEASE

On no occasion was any evidence of the disease found in adult shearwaters. Relatively small numbers of adults were examined in 1948 and 1949, but in 1950, 370 adults were examined between 5 and 10 August and none showed signs of the disease. Three of these adults had large flat warts on the webs of their feet, but attempts at transmission of such warts to ducklings gave negative results. In 1950 the first juvenile was not seen in the open till 10 August. In Table 3 the number of diseased juveniles of different

Table 3. *Infection-rate among juvenile shearwaters of different ages in 1949*

Amount of down	Approximate age (days)	Number examined	Number infected	% infected
++	60–65	102	2	2
+	65–70	162	7	4
0	70–75	964	220	23

ages is shown. In the very downy birds which would only recently have begun making excursions from their burrows the disease-rate was 2%, while of those with small amounts of residual down 4% were infected. Among juveniles without residual down 23% showed blistering of the webs. (These figures were taken from all the areas where any diseased birds were found in the 1949 survey.) Both field observation and laboratory experiments suggest that the incubation period of the disease is from 3–7 days. It therefore seems reasonably certain that the vast majority of the juveniles became infected after they had been deserted by their parents and usually after they had begun to move away from their nesting burrows at night.

Normally the first sign of the disease was the appearance of one or more small inflamed patches in the webs of an otherwise healthy bird. Within 24 hours blisters containing considerable volumes of opalescent fluid were present. Occasionally infected birds died in the first 24 hours after the appearance of the blisters, but usually they survived longer, and the evidence both from field recoveries and from birds taken into the camp

and observed in cages was that the commonest time of death was 3–4 days after the onset, but that the disease might take a week and possibly as long as 10 days to progress to a fatal outcome. In 1948 and 1949 many of the sick birds showed conjunctivitis with a small amount of purulent exudate and eyelids stuck firmly together when they were moribund. In 1946 this had been a more severe and regular feature of the disease, but in 1947 of eighty sick birds examined not one had any sign of conjunctivitis. Occasional birds showed extensor spasm of the legs in the late stages of the disease. Lung lesions were less common than in 1947 and most birds which were examined post-mortem had no obvious macroscopic abnormalities of their internal organs. We have seen one bird which recovered completely and others which appeared to be recovering, but relapses were common with further crops of blisters. Of nine sick birds observed in cages in

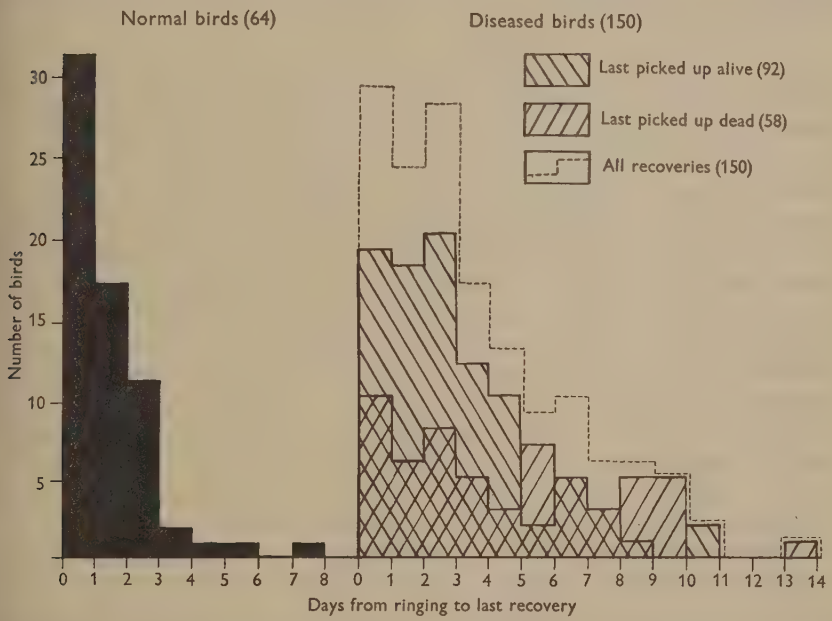
Normal birds (64)
Diseased birds (150)
Last picked up alive (92)
Last picked up dead (58)
All recoveries (150)
Number of birds
30
25
20
15
10
5
0 1 2 3 4 5 6 7 8 0 1 2 3 4 5 6 7 8 9 10 11 12 13 14
Days from ringing to last recovery

Fig. 2. The times of recovery of normal and diseased juvenile shearwaters after initial ringing in 1949.

the camp area during these years, seven died, and two appeared to have recovered when they were eventually released. These results, together with our field observations, lead us to suggest that the fatality-rate of the disease in juvenile Manx shearwaters is over 75% but that recoveries do occur.

THE MORBIDITY-RATE

When birds are moribund they are naturally very slow in making their escape, but otherwise there is no great difference in the ease with which healthy and diseased birds are captured. We think that our figures (see Table 1) do not grossly distort the picture of the number of infected birds present on any one night. When we attempt to decide what percentage of birds becomes infected before leaving the island the problem is much more difficult. Fig 2 shows the periods from first ringing to last

recovery in normal and diseased birds. The birds last picked up dead are shown separately since in some cases they were missed for 24 hours or more after death, before being found. It is clear that diseased birds do not readily leave the land and that a false high estimate of the morbidity-rate would be given by our figures for North Valley and the Wall area in Table 1. An unknown factor is the number of juveniles that leave the island whilst still incubating the disease; in some areas this number may well be high. We conclude that in all probability the percentage of juvenile shearwaters developing signs of infection in 1949, in North Valley and in the Wall area, was somewhere between the figures given in the two percentage columns of Table 1, and in 1948 rather lower than the figures given in the same table. In other areas our figures are probably under-estimates of the infection-rate except in those areas where it was certainly very low.

THE ORIGIN AND MODE OF SPREAD OF THE VIRUS

We have already given evidence that adult shearwaters probably do not suffer from the disease, or at any rate only very rarely, and that the juveniles usually become infected after they have been deserted and after they have started to make their nocturnal excursions. As we will show later, it is highly probable that during the epizootic the disease is spread from bird to bird by direct or indirect contact; but the source of the infection which starts an epizootic is not so easy to discover. Our first theory was that Trombiculid mites might play some part in the spread of the disease and perhaps act as an inter-epizootic reservoir. A pool of mites from infected shearwaters was shown to contain virus after having been kept for 6 weeks at room temperature. However, morphologically similar mites from rabbits and field mice (*Apodemus sylvaticus*) trapped in North Valley, did not contain virus either in the epizootic period in 1948, nor earlier in the year in 1950. A small number of normal and diseased birds was examined for the presence of Trombiculid mites around the vent. Young birds showed less infestation than older birds, but the number of mites present on diseased birds did not differ significantly from that present on normals.

Another possibility was that the original shearwater cases might have acquired their infection indirectly from sick gulls. Lesser black-backed gulls (*Larus fuscus*), herring-gulls (*L. argentatus*) and great black-backed gulls (*L. marinus*) are all common on Skomer, particularly the first mentioned. They prey on the juvenile shearwaters and frequently alight among the burrows of a colony when searching for birds which have failed to take cover at dawn. Sick juvenile gulls, some with lesions on their feet, were reported during August both on Skomer and Skokholm in the years 1947–9. On Skomer early in August 1950 we caught an apparently healthy adult lesser black-backed gull with blisters of fairly long standing on the webs of both feet. We failed to transmit the disease with material from these blisters to juvenile shearwaters. In the first week of September one of us found a sick juvenile gull (probably *L. argentatus*) on Fair Isle with acute blisters. Material from these blisters, free from viable bacteria, produced typical blisters on the webs of two shearwaters. We have no absolute proof that this virus is the same as those we had previously obtained from shearwaters because we had lost the old strains, and the artificially transmitted virus caused only mild disease in the two inoculated shearwaters. Though our evidence is

scanty we suggest, tentatively, that puffinosis may be primarily a disease of gulls of several species and exist over a wide area. Thus a shearwater treading on ground recently contaminated with blister fluid from an infected gull is liable to become infected and may, under suitable conditions, initiate an epizootic. The fact that most of the cases of puffinosis on Skokholm were found a few hundred yards from the house, is of interest. It is in this area that the sick gulls walk around, cunningly placing themselves between the twin dangers of man and of their fellow gulls.

THE DEVELOPMENT OF AN EPIZOOTIC

The course of the 1948 and 1949 epizootics and the general distribution of the disease suggest that certain conditions are necessary for the development of an epizootic. In the first place a source of infection must be present, and this is clearly so on Skomer and Skokholm since cases occur regularly on both islands. (We have not received any reports of the disease from other breeding areas.) However, although cases occur on Skokholm no epizootic has been seen, whereas there has been one every year, at least from 1946 onwards, on Skomer. It is noteworthy that the incidence on the open coastal areas of Skomer was similar to that on Skokholm and strongly suggests that the presence of dense cover is necessary for the development of an epizootic. This is confirmed by the fact that the highest incidence of the disease was in the areas with the most dense cover such as the Wall area and the North Valley; and also by the fact that in 1948, a wet year when cover was particularly thick, the epizootic was more intense than in the dry 1949 when the growth of bracken was much less vigorous. However, on parts of the Neck where cover is extremely dense no diseased birds were found. In this area there are few breeding birds, which suggests that a high concentration of birds in an area, together with heavy cover, is essential for the development of an epizootic. Certainly we found that wherever the local morbidity-rate was high the concentration of birds in an area was also high. The reverse was not always true. Some crowded areas showed a low morbidity-rate, but such areas were usually fairly open, with little dense cover. In densely covered areas such as North Valley and by the Wall where juvenile birds may travel 25–50 yards to reach the few open spaces and where the concentration of birds is very high, there is considerable competition for the use of certain favourite boulders as pedestals for wing-flapping exercises. Also many birds may use the same track through the thick bracken. As a result blister fluid from an infected bird can contaminate the webs of several normal birds and the chance of infection is high. In such areas once the infection has been introduced an epizootic is likely to occur.

THE HISTORY OF THE DISEASE

The first record of disease among shearwaters on Skomer appears to have been made in 1908. Gurney (1913) wrote 'Mr Drane remarks (in litt.) "It is certain the Manx shearwater dies in autumn from some not obvious cause. In September 1908 hundreds lay dead on Skomer Island". This may have been due to an epidemic.' It seems probable that Mr Drane had witnessed a puffinosis epizootic. The next record of the disease on Skomer was in 1946, though there is no evidence that epizootics did not occur in the intervening years. From 1946 until 1949 and again in 1952 we observed

epizootics on Skomer, in each of which many hundreds of birds died, and we had reports of similar outbreaks in September of 1950 and 1951. Thus for the last 7 years and possibly for 45 years or more, severe annual epizootics have occurred among the juvenile shearwaters on Skomer.

The effect of these yearly epizootics on the shearwater population of the island is difficult to assess because accurate population counts have not been possible, but during the last 7 years we have noticed no obvious alteration in their numbers, nor have we noticed much variation in the extent or severity of the epizootics. The relationship between the shearwater population as a whole and the disease appears to have been remarkably stable from year to year. At first sight it seems odd that a slow-breeding bird like the Manx shearwater should be able to withstand such repeated heavy losses amongst its juvenile population without any visible effect on its total numbers. However, a somewhat comparable situation exists on those islands where the young of shearwaters and other sea-birds are taken every year by man for food. Fisher (1952) has noted that on certain islands the fulmar (*Fulmarus glacialis*) can withstand severe depredations at the hands of man without its total numbers declining, and the same appears to be true for the shearwater where its young are taken. On many of these islands the toll of young birds taken by man is probably heavier than that caused by puffinosis among the shearwaters of Skomer. Though we consider that any marked increase in the shearwater population of Skomer is unlikely because a high concentration of birds favours the spread of the disease, we do not consider that any decrease in population due to the continued epizootics will necessarily occur.

ACKNOWLEDGEMENTS

It is a pleasure to express our thanks to Mr R. Codd for his helpful co-operation on Skomer, to Mr P. Conder and Miss J. Keighley for the observations they made on Skokholm and to our various friends who have helped us at different stages of this investigation.

SUMMARY

1. Puffinosis epizootics among juvenile Manx shearwaters on the island of Skomer in 1948 and 1949 are described.

2. The course of the disease in the juvenile shearwater is described and it is concluded that the case-fatality-rate is over 75% and that the disease most commonly progresses to death in 3 to 4 days.

3. The higher incidence of the disease in certain areas in 1948 as compared with 1949 is attributed to the wet summer and the very dense cover present in the former year.

4. It is concluded that the disease can only reach epizootic proportions in an area where the population density of birds is high, and where crowding is accentuated by thick cover on the ground.

5. Evidence is presented that puffinosis may also be a disease of gulls, and that the original cases in a shearwater epizootic may acquire the disease from sick gulls.

6. The history of the disease is reviewed, and its effect on the shearwater population is considered.

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NOTES ON THE DISTRIBUTION OF THE GREY SQUIRREL (*SCIURUS CAROLINENSIS*) AND THE RED SQUIRREL (*SCIURUS VULGARIS LEUCOURUS*) IN ENGLAND AND WALES FROM 1945 TO 1952

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(With 2 Figures in the Text)

INTRODUCTION

The distribution of squirrels in England and Wales for the period from August 1944 to December 1945 has been outlined in a previous paper (Shorten 1946). It was hoped that the information from the 9495 parishes covered during that survey might serve as a basis for further studies. The spread of the introduced squirrel appeared to be affecting the distribution of the native species.

Records have been kept of reports of grey squirrels seen in new localities since 1945. During 1950–52 the distribution of both species was again surveyed in those counties where the grey squirrel was extending its range. The results are summarized and mapped here; detailed information is deposited at the Bureau of Animal Population in Oxford. The collection of the material used in this paper was made possible by the co-operation of the Infestation Control Division of the Ministry of Agriculture and Fisheries, and their county representatives; by Natural History Societies in Dorset, Lincolnshire, Yorkshire, Lancashire and Westmorland; and the West Wales Field Club. Among the many individuals who gave help I am particularly grateful to Mr J. H. Barrett (Pembrokeshire), Mr W. R. P. Bourne (Cambridgeshire), Mr E. Blezard (Cumberland), Major A. W. Boyd (Cheshire), Mr O. Hook, and keepers, for the New Forest, Mr H. G. Hurrell (Devon), Dr T. T. Macan (Westmorland), Mr W. K. Marshall (Derbyshire), Dr K. B. Rooke (Dorset), and Mr J. Staton (Nottinghamshire). A number of people answered an appeal for information published in *The Times*. My thanks are due to Mr Charles Elton and the Bureau of Animal Population for helpful advice and facilities provided during the work.

METHODS

Twenty counties and the West Riding of Yorkshire were surveyed by members of the Agricultural Executive Committees, who also provided a general report on the situation in Durham, Westmorland and Cardigan. Independent observations from members of natural history societies and from other residents in these counties were incorporated. Dorset was covered by Dr Rooke and members of the Dorset Archaeological and Natural History Society.

The questionnaire forms used by the Agricultural Executive Committees asked whether the red or the grey squirrel was present or absent during the years 1950–52

in named parishes within the county surveyed; they also asked whether the squirrels were resident or thought to be strays. When all the known facts had been given, the rest of the parishes in the county were assumed to be without either species of squirrel.

The mapping of these reports was carried out in the same way as in the 1944–45 survey; parish maps of each county were first marked, then the records were transferred to a map of smaller scale by using the National grid system. Grid squares in which no positive information had been gathered were left blank.

No comprehensive survey was carried out in Scotland and Ireland, but some records are given of grey squirrels in these countries. The red squirrel is still present in some areas within the main block of grey squirrel territory.

RESULTS

Fig. 1 shows the known distribution of red squirrels in twenty-three counties and in the West Riding of Yorkshire. Within the area covered there are 352 grid squares from which they have been reported since 1945, and 240 squares from which they seem to have disappeared. Fig. 2 gives the distribution of grey squirrels over the same area. A few new records which came in from districts outside the main census area are included in this map. 199 new grid squares have been added to the distribution, 191 being within the census area. Some of the stray individuals seen in new localities were trapped or shot, so that it remains to be seen whether all the territory gained will be held or not.

There have been four records of grey squirrels in Westmorland. In 1944 one was trapped about half a mile south of Brough; in 1947 one was shot one mile east of Kendal; a female was trapped on the Veteripont estate in Murton parish in 1949, and in 1930 another was reported to have been shot at Brough. There does not appear to be a resident population in this county yet. In Lancashire two have been shot, one on the Huntroyde estate near Burnley at the end of 1950, and one at Mitton Hall in May 1952. It is said that a pair of greys were liberated at Little Mitton in 1937, but nothing was heard of them in the interval. Huntroyde is quite close to Mitton, so that these greys may either be descendants of the Mitton pair, or they may have come in from Yorkshire.

The advance to the west through Wales has been continuing rapidly. In Denbighshire two greys were killed at Eglwysfach on the border of Caernarvonshire, in Merioneth one was killed at Llanuwchllyn, and in Montgomeryshire a grey squirrel was trapped on Garnedd Wen at a height of 1716 ft. above sea-level in 1947. Cardigan, which has hitherto been quite free of greys, reported the first one killed at Llangoedmor near Cardigan in January 1950.

Between 1945 and 1952 the squirrels have advanced from Brecon across Carmarthenshire and west to the Pembrokeshire coast at Nevern. In this county the westerly limit runs through the parishes of Treffgarne, Rudbaxton, Usmaston, Boulston and Cosheston. The farthest west they are reported to have reached in Glamorgan is Margam Park, near Port Talbot; they are also at Rhigos and Glyncorrwg.

In the south-west they have reached Porlock in Somerset, and in Devon they have been reported at Huntsham on the Somerset boundary and at Tavistock on the boundary with Cornwall. A few have been recorded in south Devon in the neighbour-

hood of West Alvington, Plymouth, Brixton and Yealmpton, and in the north-west of the county at Bishops Tawton, High Bickington, Atherington and Tawstock. Dorset has been completely traversed.

It is interesting to find that there has been an extension eastwards in Essex. The eastern boundary had remained relatively unchanged from 1937 to 1945, but now the

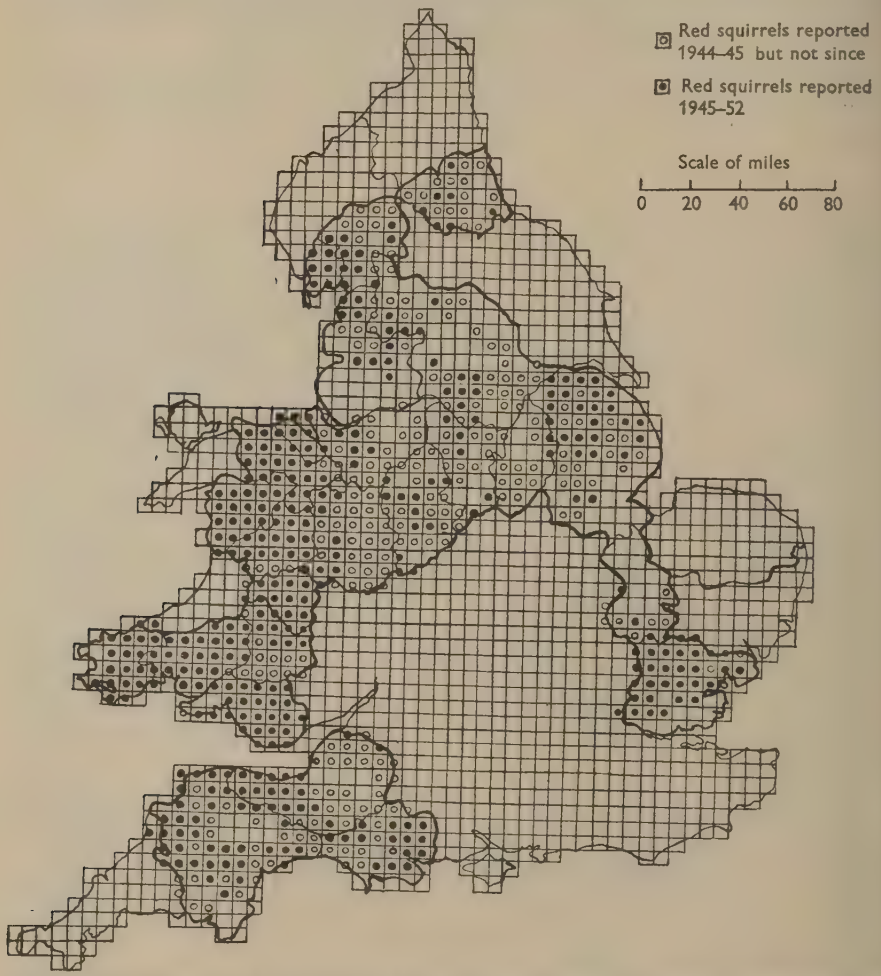

Fig. 1. The distribution of the red squirrel (*Sciurus vulgaris leucourus*) in twenty-three counties and the West Riding of Yorkshire. The squares are those of the 10 km. (National) grid; the boundaries shown are those of counties.

grey squirrel has been found as far east as Wickham Bishops, Woodham Mortimer and Ulting in Essex. The Cambridge distribution is reported to be almost unchanged, but some were killed on the Suffolk boundary at Herringswell (1947) and Thurlow (1948). Stray individuals have been seen in the Holland area of Lincolnshire at Kirton, Swineshead, Surfleet, Gosberton and Spalding, and one was killed at Terrington

St Clement, near Kings Lynn, in Norfolk, at the end of 1950. It seems improbable that a resident population will arise in this fen country.

The Lindsey division of Lincolnshire has several scattered districts which have reported the presence of grey squirrels. They have been seen at Bradley and Barnoldby-le-Beck, at Willoughton, Glentham, Appleby, Thonock, South Ormsby, Goltho and

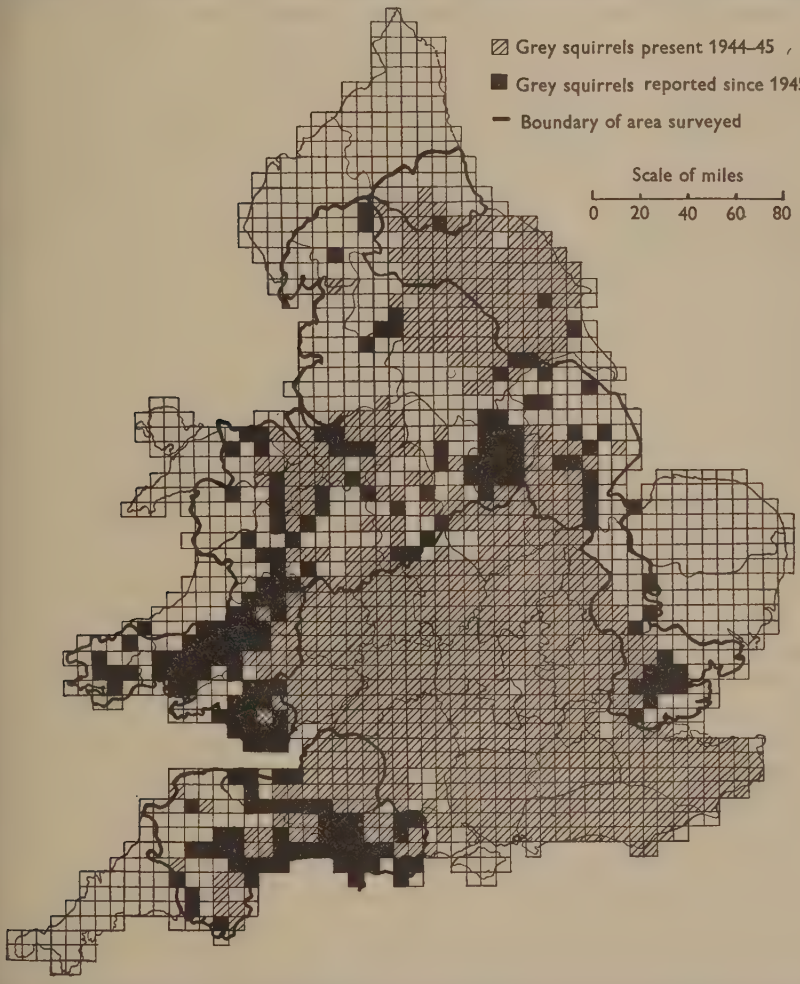

Fig. 2. The distribution of the grey squirrel (*Sciurus carolinensis*) in twenty-three counties and the West Riding of Yorkshire to show the districts into which it is known to have penetrated since 1945. County boundaries and 10 km. (National) grid are shown.

Revesby. A recent record near Candlesby confirms the isolated report in the previous survey of grey squirrels at Gunby. There has been a considerable increase in the distribution in Nottinghamshire, but in Derbyshire, Staffordshire and Shropshire there has been no striking change. In Cheshire the populations arising from separate introductions have at last joined up across the centre of the county.

Nothing more has been heard of the grey squirrels which appeared near Alnwick in Northumberland in 1930, but Suffolk has reported the presence of stray individuals in the western half of the county. Four were shot here during 1947 and 1948. There are now only three counties in England and Wales (excluding the Isles of Anglesey and Wight) which have never reported the presence of the grey squirrel; these are Caernarvonshire, Cornwall, and Cumberland. All have grey squirrels at their boundaries, and although the first arrivals have been dealt with, these counties and Cardiganshire will have to be included in the next survey.

Apart from the red squirrel records mapped in Fig. 1 some information was received about the status of this species in other counties. It is said to be still very abundant in the north part of Cardiganshire, but in Cumberland numbers have been greatly reduced round Carlisle (the reason is unknown), and it has largely disappeared at Langworthy and Skirwith on the eastern border. It is still found on old peat mosses at Scaleby, Orton, Moorthwaite and Cumwhitton, and at Great Mell Fell it ranges up to 1500 ft. It was particularly common at Dovenby until about 1940 when most of the woods there were felled.

In 1950 there was an unconfirmed report of two reds at Beaconsfield in Buckinghamshire and one was seen at Stowe during the last five years. It is still present at Lelant in Cornwall, at Llanover in Monmouthshire, Downton in Wiltshire, and at Little Aston and in Cofton Woods in Warwickshire. There was said to be a colony of reds near Uxbridge (Middlesex), and in Hertfordshire some were reported at Radlett and one was shot in mistake for a grey squirrel in 1946 at Fanshaws, Hertford. Groby (Leicestershire) and Fittleworth near Pulborough in Sussex reported the presence of red squirrels in 1948 and 1951 respectively. In Norfolk they occur in the Waveney Valley, at Lenwade, South Wotton, Great Hautbois, Fakenham, and between Wells and Holkham where they have been seen along the shore. In Suffolk they are numerous at Saxmundham, and quite common between Aldeburgh and Felixstowe; they are plentiful round Higham, Shelley, and Hadley, and numerous at Leiston. Records have come in from Great Glentham, Sudbury, Ickworth Park, Buckland, Elvedon, Brandon, near Mildenhall in the Tuddenham—Cavenham area, and from the Wickham Market—Framlingham—Chorsfield district. In Epping Forest the red squirrel is now outnumbered by the grey but there has been a small increase in numbers at Monkwood.

Red squirrels were reasonably numerous in the New Forest area until about 1939 but since then numbers have declined. In the vicinity of Burley and Lyndhurst they were well distributed everywhere until 1944, but between then and 1947 they disappeared completely. At Sway there were always a few until 1944; the last one here was found in 1947. In the Shave Green neighbourhood there have been very few since grey squirrels moved in; there was a pair left in Oakley in 1949. After 1943 they were practically extinct in the Stockley district, and on the Marchwood estate none have been seen since 1946, although before that there were always two or three pairs. Within a ten-mile radius of Woodlands red squirrels have declined rapidly in numbers, so that there are now only about two pairs in the neighbourhood. They have been seen at Irons Hill and at Brockenhurst, but have quite gone from the Beaulieu Manor estate. There were no other reports of red squirrels in Hampshire besides these. The list of

red squirrel localities given above has been compiled from chance records, and does not represent a survey of their distribution in the counties mentioned.

Black squirrels, thought to be colour variations of the red squirrel, have been reported from several places. A specimen from Carnethy, Penicuik, Midlothian, was identified by the British Museum as probably belonging to the Austrian race of squirrels. In 1949 a black squirrel was seen in the Waveney Valley in Norfolk, and in 1951 one or more appeared in the Barnston Dale district in Cheshire. Near Rostrevor in Co. Down a 'pure black' squirrel was seen in 1950.

Little is known about the present distribution of the grey squirrel or the red squirrel in Ireland. Since the grey was introduced at Castle Forbes in Co. Longford it has been reported from Leitrim, Roscommon, Westmeath, Wicklow and Cavan. Miss Roche, of the Department of Education in the National Museum of Ireland, informs me that there is no evidence that the species is yet established in Wicklow, but it is well established at Ballymahon in Co. Longford, on the opposite border of the county from the point of introduction, and still increasing. It is abundant round the wooded shores of Lough Ree (Shannon) and is present on the north side of Loch Sheelin in Co. Cavan. The red squirrels in Ireland are the light-tailed variety found in the British Isles. Since their re-introduction in the nineteenth century they have spread into every county, but in 1938 they were reported by Moffat (1938, p. 89) to be almost extinct in parts of Cork, Wexford, Westmeath, and Antrim: 'not to mention Longford, where the alien Grey Squirrel. . . seems to have taken their place.'

In Scotland greys have been reported in the country round Dollar (Clackmannan), Muckart and Drumearn (Perthshire), Kilcreggain on the west bank of the Clyde opposite Greenock, at Falkirk, and around Edinburgh. One was shot near the south-western end of Loch Shiel.

DISCUSSION

A comparison of maps 1 and 2 will show that in fifteen of twenty-three counties surveyed, and in the West Riding of Yorkshire, the red squirrel is reported to be present over a smaller area. The distribution remains largely unchanged in the counties of Denbigh, Carmarthen, Essex, Glamorgan, Merioneth, Montgomery, Pembroke and Radnor. In some of the counties where the distribution has become limited there appears to be a correlation between the areas where grey squirrels have been present since 1945 and the areas where red squirrels are no longer reported. This is particularly noticeable in Brecon where only twenty-eight of the eighty-nine parishes report red squirrels, and in Cheshire, Cambridgeshire, Flint, Lincolnshire, Nottinghamshire, Somerset and the West Riding.

It was found during the 1945 survey that red squirrels were absent from 66% of the grid squares that had been occupied by grey squirrels in 1930. Neither species has a continuous distribution: bare moorland, fenland, and industrialized areas are not suitable as habitats for squirrels. Even a well-populated county will contain parishes with no woodlands, which are unlikely to report more than an occasional stray individual. No attempt has been made to complete and confirm the negative evidence in this survey. Positive records were mapped, and the areas which did not report squirrels were left blank. Some of the grey squirrels in Wales showed evidence of disease during the period of the survey.

SUMMARY

1. During the years 1945–52 the distribution of red and grey squirrels was surveyed in twenty-three counties and the West Riding of Yorkshire. The results are given in maps marked with the county boundaries and the 10 km. National grid. New records of the presence of the grey squirrel show it to have spread into a further 199 squares. The red squirrel was not reported from 241 squares in which it was said to occur in 1944–45.

2. In eight counties red squirrels would seem to have disappeared from areas where grey squirrels have been established since 1945.

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ORIENTATION AND AGGREGATION IN *BALANUS BALANUS* (L.) DA COSTA

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(With Plates 2 and 3 and 4 Figures in the Text)

Dense communities of littoral and sublittoral barnacles are well known; in seasons when larval output is high the cyprids often settle on established barnacles whether these belong to settlements of previous years or to an earlier settlement of the same season (see, for example, Barnes & Powell 1950*a*). The presence of individuals upon one another in such species as *Balanus balanoides* (L.) and *B. crenatus* Brug. appears, from the available evidence, to be largely a matter of space limitation, although it has been suggested that under these conditions the cyprids of both species are less 'selective' in their settling reactions. It would seem that the very characteristic colonial aggregations found in other barnacles, from widely different species, constitute a somewhat different phenomenon. For example, such colonial aggregations have been figured for *Scalpellum sociabile* Annandale (Annandale 1909), for *Balanus hameri* (Asc.) (Moore 1935) and for *Tetraclita* sp. (see Pilsbry 1916, plates 58–60). Apparently similar aggregations are often found in *Balanus balanus* (Pls. 2 and 3).

In the Firth of Clyde, *B. balanus* is fairly common on suitable bottoms; it is found particularly on stones and mollusc shells, both living and dead, in the sublittoral region down to at least 20 fathoms, and may be readily obtained by dredging. The material collected from stones is often very badly misshapen, since the small stones on which the spat settle are not large enough for normal growth to take place over long periods. Further, nothing is known about the position on the bottom of such material. For this study particular attention has been given to the epizoic barnacles on large clams, *Pecten maximus* (L.). On such living material, whose orientation on the bottom is known, settlement of *Balanus balanus* is often only moderate in density, and more or less normal growth of the barnacles may take place over a number of years.

(*a*) *Space limitation and aggregation*

An examination of a large number of shells with epizoic *B. balanus* has clearly shown that the formation of aggregations is not merely the result of space limitation. This is illustrated in Pls. 2 and 3 in which many characteristic aggregations of barnacles are shown, although there is considerable barnacle-free shell surface available for settlement; the absence of calcareous bases around the aggregations indicates that this does not arise from a very heavy settlement with subsequent loss by breaking away as described for other species by Barnes & Powell (1950*a*). Further, these aggregations are, so to speak, cumulative and contain individuals from several successive year-groups so that they resemble those described, for example, for *B. hameri* by Moore (1935).

In Pl. 3*A* two large aggregations are shown, each consisting of three distinct year-classes, in one case the whole colonial aggregate being made up of twenty-nine barnacles; on the original barnacle, epizoic on the clam shell, are five individuals of a later year class and on each of the latter up to seven of the next year-class. The size (carino-rostral diameter) of the individual barnacles, as well as the grouping of this colonial aggregate, is given in Fig. 1.

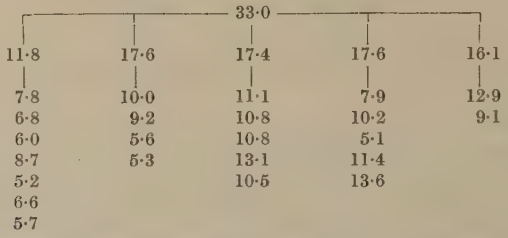


Fig. 1. Sizes of individuals in colonial agregation shown in Pl. 3*A* (top right). Figures are rostro-carinal diameter in mm.; some distortion of the younger individuals.

(*b*) *Distribution and orientation of* Balanus *on the shells*

On those *Pecten* where the number of barnacles was only moderate, inspection suggested that there was a tendency for them to be more frequent near the periphery of the shell (see, for example, those in Pl. 3*B*). To investigate this possibility each shell was divided into a number of subareas and the epizoic barnacles present in each counted and their carino-rostral diameter measured. The results are given in Fig. 2, where the percentages on each subarea are shown for three size-groups of barnacles on fifty living *Pecten*. The results for the smallest size-group (0–10 mm.) substantiate the above suggestion that there is a concentration at the periphery of the *Pecten* shells;

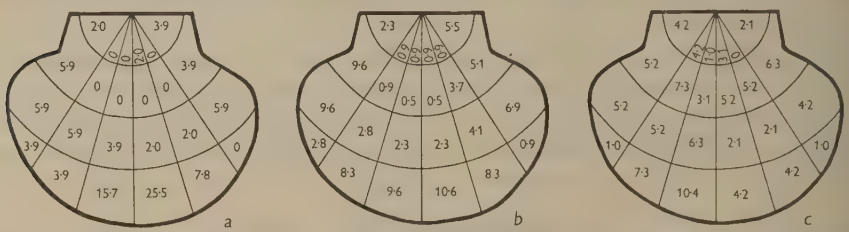
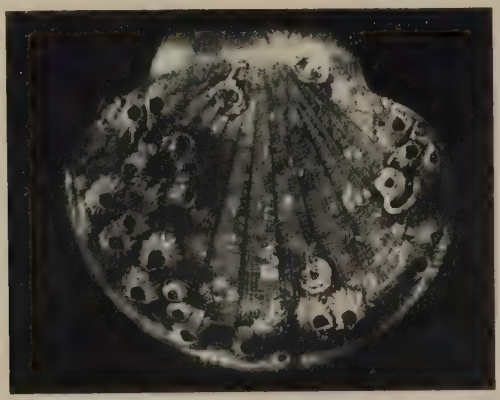


Fig. 2. Percentage of epizoic *Balanus balanus* of three size-groups on twenty-four subareas of a number of clam shells; each shell is divided into four equally spaced concentric zones and six radiating zones. *a*, size 0–10 mm.; *b*, size 10·1–20 mm.; *c*, size > 20 mm.

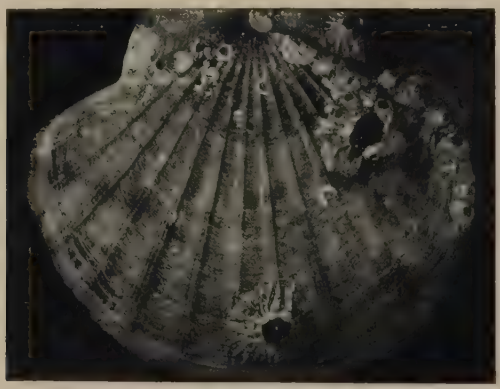
the peripheral subareas contain 84% of all the epizoic barnacles of this size-group. In the next larger size-group of barnacles (10–20 mm.) the proportion at the periphery, although still high, is less marked, whilst in the largest size-group (> 20 mm.) no concentration at the periphery is apparent. The contrast between the results for the small and large size-groups is, of course, due to the growth of the *Pecten* shell; the larger and therefore older barnacles, now present in the centres of the shells, may well have settled at what was the edge of the shell at the time of settlement. The reason for this preferential settlement at the periphery is not certain; it can hardly be due to the

Characteristic aggregates of *Balanus balanus*.

A. *Balanus balanus* on clam shells; aggregates composed of several year-classes; large aggregation of three year-classes top left (Fig. 1).



B. Very clear aggregation at the shell periphery; *Hydroides norvegica* also present. Note the major orientation of the barnacles along concentric striae (p. 143).



C. Orientation to lamellae, and ridges on the auricle (top right); some peripheral concentration; note the absence of epizoic barnacles on a solitary individual.

positive light reaction (Barnes, Crisp & Powell 1951) in the crawling cyprid, since the difference in light intensity must be very small between the two positions, particularly with the diffuse light at the depths from which the clams were taken. It is possible that the effect is due to the free-swimming cyprids being drawn to the edges from the surrounding water by the inhalent current of the *Pecten*, or even that there is a slight current over the whole shell from anterior to posterior as a result of this inhalent current and that the crawling cypris larvae are negatively rheotropic. A third possibility is preferred: in the resting condition, the valves of the clam shell are open and by dropping a clam shell through water it has been found that the average angle to the horizontal of the upper valve, measured in the median plane, when the clam comes to rest and opens is about 15°; a peripheral concentration of the epizoic barnacles could

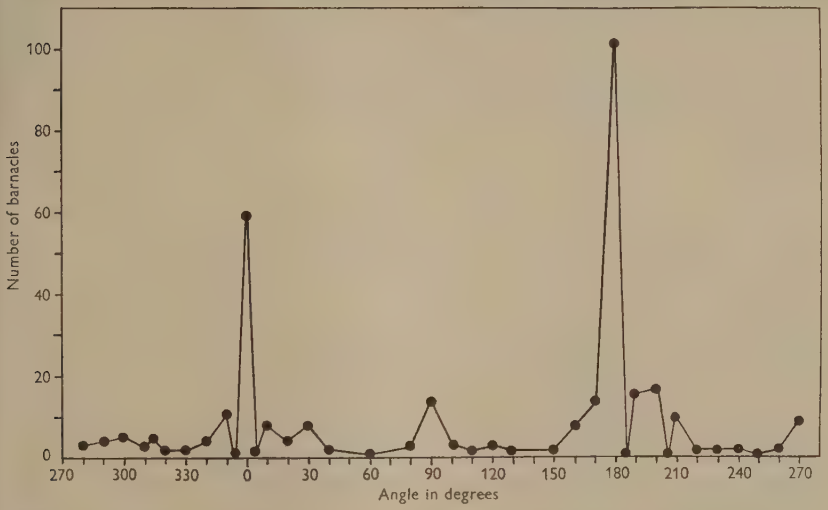


Fig. 3. Orientation of barnacles to concentric lamellae. Frequency distribution of the angle between the rostro-carinal axis and the tangent to the lamella at centre.

therefore arise if the crawling cypris larvae have a negative reaction to gravity. This suggestion is supported by examination of other dredged material; the positions of rest on the bottom with such material is, of course, unknown, but the frequent occurrence of barnacles on what may be supposed to be elevated parts of stones and shells is conspicuous. Further, there is often a tendency on shells such as *Chlamys opercularis* (L.), where the upper valve is also curved, for the barnacles to be concentrated at the highest part of this valve. In a bottom- but not mud-living animal, such a negative reaction to gravity could have distinct survival value.

Inspection also shows that the epizoic barnacles tend to have an orientation whatever their position on the shell, and in general they lie with their carino-rostral axis along the conspicuous concentric lamellae. The angle between the carino-rostral axis and the tangent to the lamellae at the centre of the barnacles has been measured: a barnacle lying with its axis along the tangent is taken as being at 0 or 180° according to whether the carina is to the left or to the right; at 90 and 270° the barnacle is at right

angles to the tangent, that is lying across the lamella. The distribution of these angles for about 200 barnacles of all size-groups is given in Fig. 3. Clearly the majority lie with their axes along the tangent to the lamellae, that is, at either 0 or 180°. Now the grooves formed by these concentric lamellae are comparable in size with the cyprids, and it is suggested that this orientation is the result of a tactile response of the cyprid (Barnes *et al.* 1931) to the concentric grooves. It is noticeable that this orientation to the concentric rings breaks down in two places: first, on the auricles (see Pl. 3*C*) where the barnacles are often orientated in the grooves formed by the coarser linear ribs, and secondly on the dorsal and narrow part of the valve where it adjoins the auricles. At this latter point the ribs radiating from the umbal region are both small and close together so that the grooves between them are narrow; here orientation is often to these narrow grooves rather than to the less well defined and finer striae.

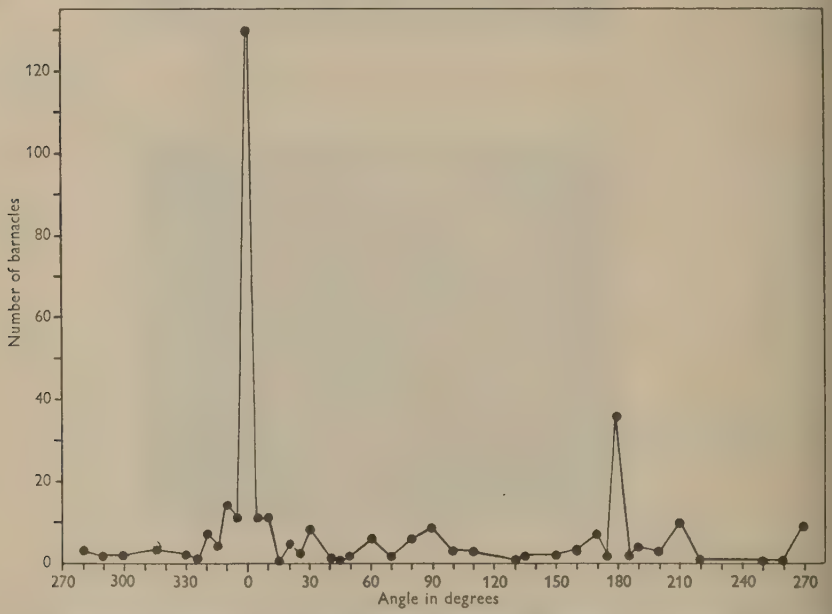


Fig. 4. Orientation of barnacle to grooves of larger barnacles. Frequency distribution of the angle between younger barnacles and the groove in a plane tangential to the surface.

(*c*) *Orientation of the younger barnacles in the colonial aggregates*

The compartments of *Balanus balanus* are grooved externally in a characteristic manner and, in view of the foregoing, orientation of the younger barnacles in the grooves of the older might be expected as a result of its tactile responses. The angle of the younger barnacles was therefore measured in relation to these grooves. The orientation angle was measured in the plane tangential to the surface at the groove, no account being taken of the position around the circumference of the older barnacle, and the direction of the groove was taken as 0° upwards and 180° downwards. A barnacle lying along a groove would therefore again be at either 0° or 180° according to the position of the carinal end, 0° when the latter was upwards towards the opening of the

lder barnacle. The results are given in Fig. 4. It is clear from the figure that the arnacles are orientated along the grooves, so that the majority occur either at 0° or 80°. Further, in contrast to the orientation with respect to the concentric striae, the rientation at 0° is very much stronger than at 180°. It should also be pointed out that hese orientated barnacles tend to be much more frequent on the upper part of the lder individual. Indeed, as can be seen from the plates, there is a distinct tendency or them to cluster round the upper periphery.

The tendency for accumulation in the grooves can be explained as a result of nechanical stimulation and both thigmo-taxis and thigmo-kinesis may be involved. \ thigmo-tactic reaction would tend to keep the cyprid in the groove, once the groove iad been encountered during random movement, and a low thigmo-kinesis could)ring the animal to rest in the groove. From unpublished results it is known that :yprids of other species certainly exhibit low thigmo-kinesis as distinct from thigmo-axis. The accumulation in the upper parts of the groove and the stronger orientation o 0° can then be explained as a result of thigmo-taxis, since a cyprid crawling over the :lam surface will encounter the groove at the lower part, where the groove meets the

Table 1.

	Carinal	Rostral		Carinal
Quadrant ...	1	2	3	4
Numbers present (1)	63	100	96	75 ($P=0{\cdot}02$)
Numbers present (2)	29	95	97	31 ($P<0{\cdot}02$)

hell at the base of the older barnacle, and a thigmo-tactic response would keep it noving in the groove until fixation ensued. Final fixation and metamorphosis could hen take place in the upper part of the groove, the ultimate cessation of movement)eing influenced by a thigmo-kinetic response. (It should, of course, be remembered hat cessation of crawling takes place even in the absence of grooves in a cypris larva.) There is no need to postulate a negative gravity response to explain the accumulation t the upper periphery, although such a response, as has already been suggested, may n addition be present. That a negative response to gravity is not necessary for such an :ccumulation is indicated by similar peripheral accumulation on barnacles growing on 'ertical panels, in which case the movement to the upper parts of the barnacle is roughly at right angles to the gravitational force.

There is also an orientation of the younger barnacles around the older barnacles in hese aggregations, most readily seen by looking down upon the cluster from above, ind this has been demonstrated by counting the numbers of epizoic young individuals n the four quadrants in the plane of the opening of the older barnacle, that is, parallel :o its basis. Table 1 shows the number of barnacles settled in the four quadrants,)btained by dividing the barnacle along the carino-rostral axis and at right angles to :his at the centre, quadrants 1 and 4 being 'carinal' and 2 and 3 'rostral'. Two sets of shells were examined and in each case the numbers are significantly different (χ^2 test) from those expected on the assumption that all the quadrants are equal as regards cypris settlement: there are significantly more barnacles in the rostral than the carinal quadrants; there is no significant difference between either of the two rostral or the two carinal quadrants considered separately.

The reason for this unequal distribution around the big barnacle with a larger number towards the rostral end does not appear to lie in the two responses already discussed, since in respect to these factors the circumference of the opening of the adult would seem to be everywhere the same. It may be due to the cirral beat. It has been shown that there is a definite current over the back of the cirri and the turbulence set up might tend to prevent settling on the carinal side. On the other hand, if the cyprids originate directly in the older barnacle (see next section) the accumulations on the rostral side may be due to their being pushed out by the movement of the body when the operculum opens and the cirri beat.

(*d*) *The origin of clusters*

The orientation of the individuals and their distribution both in relation to one another and to the mollusc can largely be explained on the basis of two types of response of cyprids; both types of response have been observed or inferred in cyprids of other species. This has not, however, completely explained why the settlement often appears to be almost confined to an adult barnacle already present on the clam whilst the surrounding and equally available surface remains quite clean. It is possible in these cases to assume an attraction, say chemical stimulus, of the cyprids by the large individuals either directly from the planktonic phase or during the crawling movements, but for such a hypothesis there is at present no evidence.

An alternative explanation may be tentatively advanced. It is possible that in some cases the cyprids which give rise to the characteristic attachment of several successive year-groups, have been developed in the mantle cavity of the barnacle to which they are attached, although most of the larvae are extruded as nauplii and develop to cyprids as free-living plankton, as is apparent in *B. balanus* by the large numbers of non-colonial individuals and the presence of the various stages in the plankton. (See Broch (1924) for a discussion of the effect of external conditions and the retention of larvae and its bearing upon problems of distribution.) There is no direct evidence for this hypothesis. Examination of ripe *B. balanus* has so far not yielded cyprids within the mantle cavity, but it is known that under some circumstances development of the nauplii beyond the stage when they are normally extruded does take place and there is a recorded instance of a cyprid of *B. balanoides* being found in the cavity (Runnström 1925). However, in other genera where similar colonial aggregations are found (*Scalpellum* (not in every species), *Ibla*, *Tetraclita* and probably *Analesma*) it is known that development of the larval stages to the cyprid does take place in the mantle cavity of the adult. It seems reasonable to assume in these cases at least that although some, perhaps most, of the cyprids are shed into the plankton, perhaps those developed earlier, others merely crawl around the parent and in this process tend to become orientated and give rise to the characteristic colonies. It is to be noted that with the exception of *Tetraclita* these are all deeper water forms which do not tend to occur in dense masses like the intertidal forms and so require ancillary mechanisms to ensure cross-fertilization. The general, although not invariable, absence of colonies on solitary individuals of *Balanus balanus*, which would presumably be sterile, supports this contention.

DISCUSSION

It is to be expected in an Order in which all the representatives are either sessile or parasitic animals in the adult stages, that tactile responses would be highly developed in the larvae. There would appear to be a distinct period during the early cypris stage when contact with a solid surface does not induce crawling reactions with ultimate settlement since, although there is no direct evidence for this, it may be presumed from the fact that there is a distinct interval between the appearance of large numbers of cyprids in the plankton and their settlement on the shore. During this period physiological changes take place so that eventually reaction to a solid surface ensues, although there is evidence from other sedentary animals that metamorphosis can be delayed if a suitable substratum is not encountered. Both the area available for exploratory movements and the resistance to pressure by the antennules of the solid surface may play a part in this phase, since it has been shown that *B. balanoides* will not settle on a surface of stiff glass fibres (Barnes & Powell 1950*b*).

The reactions to mechanical stimulation just discussed are further examples of the highly developed tactile response in these animals. These responses which in the intertidal forms are effective in securing a firm attachment to the substratum are also of advantage in ensuring cross-fertilization in the deep-water species where dense aggregations are not generally found. Even in those species, which ensure cross-fertilization by means of complemental males or which are dioecious, a thigmo-kinetic response in the males seems to be evident. Darwin (1851) described how in many species the males are embedded in a distinct position, usually of a crack- or fold-like character. In *Scalpellum scalpellum* (L.) the males are over an oblique notch in the spinose chitinous border of the scuta; in *S. ornatum* Darw. they are found in a transverse pouch on the underside of the scuta; in *S. rutilum* Darw. the cavity is formed by the scutum itself being externally convex. Similar positions have been described for the attachment of the male in other species, but whereas Darwin suggested that these pouches were found by visual perception, it would seem that thigmo-kinetic response is perhaps more likely. Further, it would seem that such responses, in an even more specialized form play an important part in the very specific epizoic relations found between the whale and turtle barnacles, as well as in specific host-parasite relations of the Rhizocephala.

SUMMARY

Balanus balanus epizoic on clam shells has been shown to be orientated with respect to the grooves of the shell and when settled on one another to be orientated within the aggregate. The orientations can result from responses to mechanical stimulation. Such responses may lead to the well-known colonial aggregates, but it is suggested that possibly in this, and more certainly in other genera development of the cyprids within the mantle cavity followed by the appropriate mechanical responses is important in the formation of colonial aggregates. The possible importance of these mechanical responses in relation to the attachment of dwarf males and of the specific epizoic relations in other Cirripede species is discussed.

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ON THE FAUNA OF A BROWN FLUX OF AN ELM TREE, *ULMUS PROCERA* SALISB.

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(With 2 Figures in the Text)

The following observations were made on an elm tree brown flux in Sheffield over a period of about two years. During this time the flux had a continuous existence and carried a fauna which formed a balanced association. The purpose of the investigations was to throw light on the ingredients of this association, its seasonal fluctuations and the interdependence of its members.

I take pleasure in thanking Prof. L. E. S. Eastham for suggesting the problem and for help during the investigation. It is pleasant also to thank Dr H. Oldroyd, Dr F. van Emden and Dr P. Freeman of the British Museum (Natural History) for identifying the flux-visiting Diptera.

THE FLUX

Records of brown fluxes and their faunas have previously been made by Ludwig (1888); Massee (1897); Ogilvie (1924) and Keilin (1921, 1927). The flux here under consideration owes its existence to an out-pouring of sap from the wound of a branch scar at the height of about 6 ft. above ground-level. The sap oozes continually, though less copiously in winter than in spring and summer. In so doing, it forms a stream over the tree bark varying in width from 9 in. to 1 ft. In this position the substance of the flux develops as a spongy mass which holds the sap emerging from the tree and thus provides a stable micro-aquatic environment to which certain organisms are attracted and in which they live and often breed.

In spring and early summer the flux is dark brown and slimy. In winter, on the other hand, the lower parts are dry and light stone-coloured—features in agreement with the findings of Ogilvie (1924). The pH of the flux material was 8·7 throughout the year. Ogilvie (1924) records a pH of a similar elm flux as 9·0–9·5. Standard tests for starches, sugars, fats and proteins yielded negative results though a polysaccharide, not starch and possibly cellulose, was indicated.

The animals inhabiting the brown flux form a characteristic fauna which is constantly undergoing change throughout the year. The members of this fauna are:

(*a*) The mite *Hericia hericia* Kramer (Tyroglyphidae).

(*b*) The larvae of the following Diptera: *Dasyhelea obscura* Winnertz (Ceratopogonidae), *Aulacigaster leucopeza* (Meigen) (Aulacigasteridae), *Brachyopa insensilis* Collin (Syrphidae), two undetermined species of *Systenus* (Dolichopodidae), one undetermined species of *Phaonia* (Anthomyidae).

(*c*) The Staphylinid beetle *Thamiarea hospita* Maerk.

Keilin (1921) recorded the following from brown fluxes of elm trees in Cambridge. Dipterous larvae: *Dasyhelea obscura* Winn., *Rhyphus fenestralis* (Scop.), *Mycetobia pallipes* Meig., *Systenus adpropinquans* Loew., *Systenus scholtzii* Loew., *Aulacigaster rufitarsis* (Meig.), *Phaonia cincta* Zett. and an undetermined Syrphid larva closely allied to the genus *Ceria*; larvae of two Staphylinid beetles, one belonging to the genus *Quedius* (subfamily Staphylininae), the other being possibly a *Thamiarea* sp. (subfamily Aleocharinae); and the mite *Hericia hericia* Kramer (Tyroglyphidae).

In 1927 Keilin also recorded the following dipterous larvae in the sap exudation of a horse-chestnut tree in Cambridge: *Dasyhelea obscura* Winn., *Rhyphus fenestralis* (Scop.), *Mycetobia pallipes* Meig., *Aulacigaster rufitarsis* (Meig.). There is thus a considerable resemblance between the elm and chestnut tree fluxes of Keilin and that of the Sheffield elm tree. Such differences as there are between the latter and the two former ones are probably attributable to geographical causes.

The seasonal sequences are shown diagrammatically in Fig. 1.

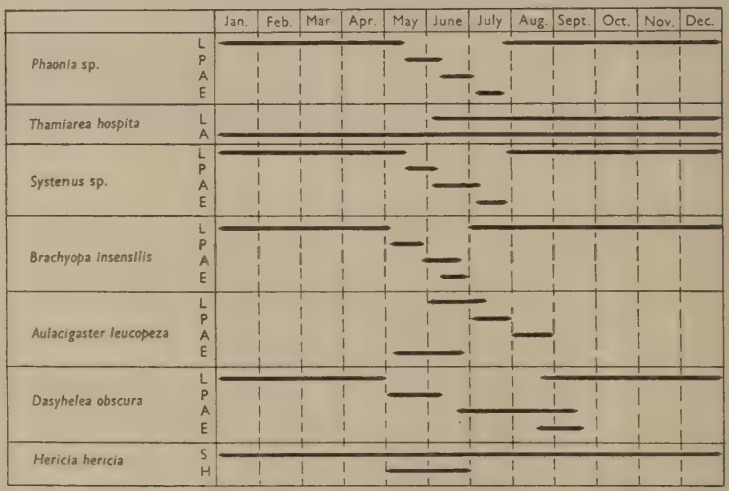

Fig. 1. The seasonal sequences of the flux-inhabiting animals. *L* = larvae; *P* = pupae; *A* = adults; *E* = eggs; *S* = all stages except the hypopus; *H* = hypopus.

Hericia hericia. All stages in the life history of this mite except that of the hypopial nymph (egg, hexapod larva, ordinary nymphs, adult males and females) are found in the flux material throughout the year. There is a seasonal increase in reproductive activity in May when an increased number of eggs is to be found. Only during May and June is the hypopial nymph found.

Dasyhelea obscura. Oviposition takes place in August and early September. The larvae live in the flux throughout the winter, pupating and emerging the following spring.

Aulacigaster leucopeza. Oviposition takes place in May and early June. The larvae live in the flux during the summer, pupate in late July and emerge in August. No larvae or pupae were seen in the flux during the winter months—only the empty puparia from the preceding summer. The absence of living stages of this species from

ne flux during winter may be accidental. On the other hand *Aulacigaster* may have ther hibernating quarters in either or both the adult and larval states; nothing is nown of this.

Brachyopa insensilis. Oviposition takes place in June. The larvae live in the flux hroughout the year, pupating and emerging in May and June.

Systenus spp. Oviposition takes place in July, pupation and emergence in June of he following year.

Phaonia sp. Oviposition takes place in June and July, pupation and emergence in he following June.

Thamiarea hospita. The adults are found on the flux surface throughout the year, as also are the larvae during the summer months.

Attempts were made to work out the feeding relationships of the animals inhabiting he tree fluxes by direct observations and by examination of the gut contents and of the structure of the animal (see Fig. 2). The larvae, ordinary nymphs and adults of *Hericia*

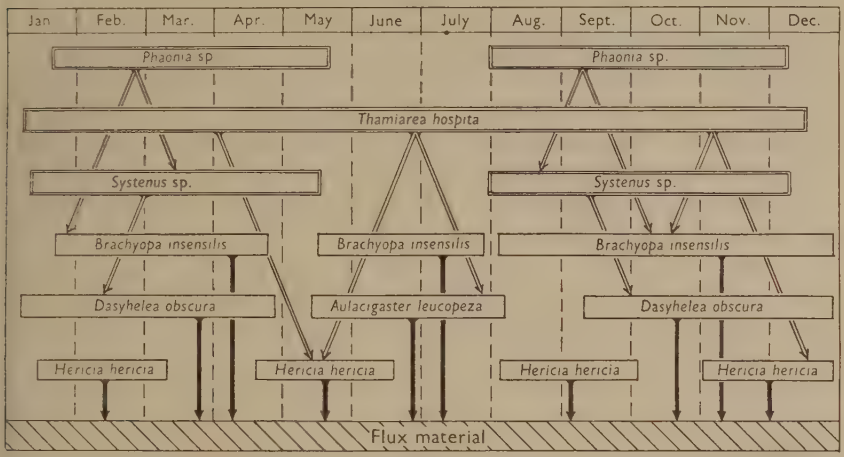

Fig. 2. The food-chain of the flux fauna. ▣, carnivores; □, flux-feeders.

hericia, and the larvae of *Dasyhelea obscura*, of *Aulacigaster leucopeza* and of *Brachyopa insensilis* are found to be saprophytic. They can be seen feeding directly on the material of the flux and are able to live for prolonged periods on flux material which has been previously heated to kill any living organisms present. They are found in the fauna of the slime flux in relatively large numbers. In confirmation of this transverse sections of larvae of *Aulacigaster leucopeza* and *Brachyopa insensilis* revealed the presence of longitudinal ridges in the floor of the pharynx, characteristic of saprophytic cyclorrhaphous dipterous larvae (Keilin 1915).

The *Systenus* larva is carnivorous, feeding chiefly on the larvae of *Dasyhelea obscura*, as many as ten head-capsules of the latter having been found in its mid-gut. Keilin (1921) reported similarly on this food habit of *Systenus*, stating that both larvae and pupae of *Dasyhelea obscura* are destroyed by *Systenus adpropinquans* and *S. scholtzii*. On occasions *Systenus* has been found to be cannibalistic. The larvae of the *Phaonia* sp. are also carnivorous, and they have been observed to attack larvae of *Brachyopa*

insensilis, *Dasyhelea obscura* and *Systenus* sp. In *Phaonia* as in *Systenus*, the pharynx floor is smooth and its cuticle thick. The adults and larvae of *Thamiarea hospita* freely devour the mite *Hericia hericia*, larvae of *Dasyhelea obscura* and *Aulacigaster leucopeza*.

Although the fauna of the flux is undergoing change throughout the year (Fig. 1) it is nevertheless a balanced association at all times. Thus there are always forms which feed directly on the flux pasturage and there are also those others which feed on the herbivores. Of the herbivores *Hericia* and *Brachyopa* are permanent inhabitants. *B. insensilis* has a prolonged larval association with the flux materials only interrupted in May and June by reproductive activity (Fig. 1). *Aulacigaster* larvae are only operative on the basal medium in June and July. *Dasyhelea obscura*, also a herbivore, is cut off from active feeding association with the flux for a period of four months from May to August. This species pupates at a time such that the newly hatched larvae of *Aulacigaster* can take its place in the food chain. All these forms provide food for the carnivores.

Thamiarea is present as an adult throughout the year and feeds mainly on *Hericia* which also is a permanent resident of the flux. *Phaonia* sp. has a life cycle which coincides with, but slightly succeeds that of, *Brachyopa* on which it feeds. *Systenus* fairly precisely coincides in its life cycle with *Dasyhelea* on which it also feeds. *Aulacigaster* has a short larval period covering the months of June and July and it is in this period that the *Thamiarea* larva is available to feed on it. Times of feeding and of reproductive activity are such that the association of individuals in this isolated environment with its steady food supply is maintained. In such a restricted environment as this problems of dispersal loom large. The brown flux appears to have a definite attraction for certain flies. For instance the following species were taken from the flux surface on 8 June 1948: *Systenus pallipes* Ross. (Dolichopodidae), *Brachyopa insensilis* Collin. (Syrphidae), *Aulacigaster leucopeza* Meig. (Aulacigasteridae), *Gymnochaeta viridis* Fall. (Tachinidae), *Phaonia laeta* Fall. (Muscidae), and *Mycetobia pallipes* Meig. (Anisopodidae). These observations suggest that flies visiting different fluxes for egg laying are the main agents of dispersal. The same might be said of the beetle *Thamiarea* in the adult stage.

Hericia presents a special problem, reference to which has been made in a separate publication (Robinson, in press). The hypopus stage of this mite is resistant to desiccation, is hydrofuge and floats easily on the flux water surface. In this position it attaches itself by means of suckers to flux-visiting Diptera which then act as vehicles carrying the mite from one flux to another.

SUMMARY

1. The elm tree brown flux exists throughout the year as a wet spongy mass in which a rich and characteristic fauna is present.

2. A precise timing of developmental processes enables a balanced relationship to exist amongst the animals.

3. The interdependence of the animals with regard to feeding and dispersal is described.

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THE ECOLOGY OF THE INSECT FAUNA OF PINE STUMPS

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(With 6 Figures in the Text)

INTRODUCTION

The ecology of the insect fauna of standing tree stumps has received little attention. Richards (1926) has briefly described the food relations of insects in pine stumps on a Surrey heath and suggested how succession may occur. Krogerus (1927) investigated the insects associated with pine stumps in Finland; he observed that certain insects tend to occur at different times after the tree is felled. A list of insects is given and their succession is discussed. Derksen (1941) dealt with the insect fauna of beech stumps and standing dead trunks in Germany. He describes the faunal succession in stumps in relation to decay, moisture and temperature. He found that although many features of the insect ecology of standing stumps and felled logs were common to both habitats, there were some differences.

Felled tree trunks and logs have been dealt with more adequately (Blackman & Stage 1924, Graham 1925), whilst Savely (1939) mentions that certain wood-boring beetles show a preference for standing stumps.

The present study deals with the insect fauna of standing pine stumps, and seeks to answer four main questions:

What is the composition of the insect fauna in this type of habitat in the chosen locality?

How does the habitat change in time as the wood decays?

What interaction is there between the insects and the environment?

Is there a characteristic temporal succession in the insect population of stumps, which may be correlated with the gradual decay of the wood?

The chosen area is situated on the Lancashire coast between Liverpool and Southport in the district of Formby. It covers about four square miles and contains extensive plantations of pine trees which were originally planted to counteract the effects of sand erosion. Corsican pine is the predominant species but small plantations of Scots pine are also present. No discrimination between stumps of the two species has been made in this paper. Expanses of sand between the pine stands are in various stages of plant colonization, leading to the subclimax formations of *Salix repens* L. and *Carex arenaria* L. Felling during the 1939–45 War left clearings in which numerous stumps occur. Thinning of the plantations and felling of complete areas has taken place over a number of years, and so stumps are in all stages of decay in the clearings and in the forest. The trees are felled by axe or saw about 15 cm. above soil level. The diameters

* Now at the School of Agriculture, University of Cambridge.

the stumps vary from 10 to 35 cm. Occasionally, dead trees blown down by the ind are left where they fall. The cut-over areas formed by large-scale felling are in arious stages of plant colonization.

METHODS

'emperature recordings were made with thermopiles in conjunction with a micro-nmeter. The thermopiles were constructed according to the method of Robinson 1931); each consisted of six copper-constantan thermocouples in series. When it was esired to take a temperature recording, a hole was bored in the stump at the chosen lace, and the hot junctions of the thermopile were inserted and sealed into the hole ith plastic wood. The instrument was left in position for 2 days, by which time it was ssumed that the temperature of the air surrounding the hot junctions had reached quilibrium. By this method, temperature recordings could be made at different evels, with the minimum of interference with the stump. The thermopiles were used or recording soil temperatures; air temperatures were recorded with a mercury hermometer in the shade.

In order to obtain an idea of the moisture content of the wood, either samples were emoved from whole stumps taken to the laboratory, or they were cut in the field and laced in air-tight tins. They were approximately 1 sq.cm. in section and 5–7 cm. long. Each sample was weighed as soon as possible after cutting to avoid loss of moisture. The samples were then dried at 110° C. until they reached constant weight. The noisture content of the wood was expressed as the percentage weight of water per ramme of dry wood.

The activities of wood-rotting fungi result in the formation of air spaces. This educes the mass of the wood, and provided that shrinkage is not severe there will be ittle change in the bulk volume, i.e. the volume enclosed by the outer surface of the vood. As decay progresses the bulk density decreases (Cartwright & Findlay 1946), ince bulk density = weight of oven dried wood/bulk volume. A measurement of the ulk density will therefore give an expression for the amount of decay which has ccurred. Bulk densities were worked out for the wood samples used for moisture leterminations. A method for the determination of the bulk volume of sound or lecayed wood involving the displacement of sand has been described by Campbell 1932). The method employed in this investigation is somewhat similar. Fine sand is acked into a 25 ml. graduated cylinder and the volume read after lightly tapping the op of the cylinder to settle the sand. The wood sample is now immersed in the sand. It is essential to ensure that it is completely surrounded before the reading is taken. The difference between the first and second readings gives the bulk volume of the wood. The average of five readings was taken for each sample. The volume could be estimated to 0·1 ml. The percentage moisture content and bulk density for each wood sample were obtained in this way.

The fungi responsible for decay in pine stumps were identified from their sporophores which appear during the autumn and winter. Stumps were marked according to the type of fungus which they contained and at a later date they were examined and the nature of the decayed wood was noted. Pine stumps were classified according to their location in forest or clearings, the extent of decay, and in the later stages of decay,

whether they contained white or brown rots. In the progress of decay of pine stumps, three phases are arbitrarily distinguished:

I	II	III
Stump firmly embedded in the soil	Stump firmly embedded in the soil	Stump loosely embedded in the soil
Wood uniformly hard throughout	Wood with few patches of decay	Wood extensively decayed with internal spaces
Cut surface a light colour	Cut surface and bark a dark colour	Cut surface and bark a dark colour
Subcortical space narrow	Subcortical space wide	Bark absent, or at least entirely separated
Cambium present	Cambium absent	Cambium absent

These three phases are used in the records and analysis of the insects inhabiting the stumps.

The pine forest area was visited regularly throughout the year at weekly intervals in the winter, and two or three times a week over the rest of the year. In the field, stumps were broken up with an axe or chisel, and any insects which were found were brought back to the laboratory. Some whole stumps were brought back for closer examination for small insects, e.g. Collembola, Psocoptera.

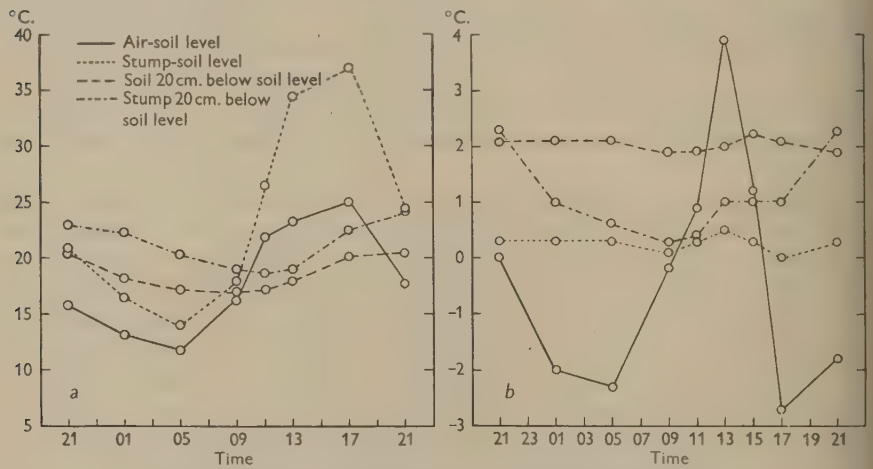

Fig. 1. Temperatures in air, in soil and in a pine stump over 24 hr.: (*a*) 30 June–1 July 1951; (*b*) 26–27 Jan. 1952.

RESULTS

(*a*) *Temperature*

The fluctuations of temperature in fallen logs have been studied by Graham (1925) and Savely (1939); both authors observed that seasonal and diurnal variations followed the trends of air temperature, although in the summer in full sunlight log temperatures reach considerably higher levels than air temperatures in the shade. Graham (1925) observed that subcortical temperatures show greater fluctuations than air temperatures, and that they vary directly with the intensity of solar radiation. No reference to temperature conditions in pine stumps has been found in the literature. Since the bulk of the stump is embedded in soil, only about 15 cm. projecting above ground, the

mperature depends on a number of factors of which the heat capacity of the medium one. The air and water content of soil (Baver 1948) and of wood will affect the heat ıpacity of the stump, and wind and precipitation will have major effects on tempera- ıre relations.

Temperature recordings were made in a pine stump in the open in winter and ımmer. At soil level temperatures were recorded in the air and in the stump, and soil ıd stump temperatures were recorded 20 cm. below soil-level. The results are xpressed graphically in Fig. 1. The June data demonstrate that during the day :mperatures at soil level are higher than those 20 cm. below the surface, but at night ıere is a reversal when the air temperature is lowest. At 20 cm. below soil level :mperature variations are less than those at the surface and stump temperatures are igher than those of the surrounding medium. Temperatures 20 cm. below lag ehind those at the surface. The January data show that in the stump, temperatures

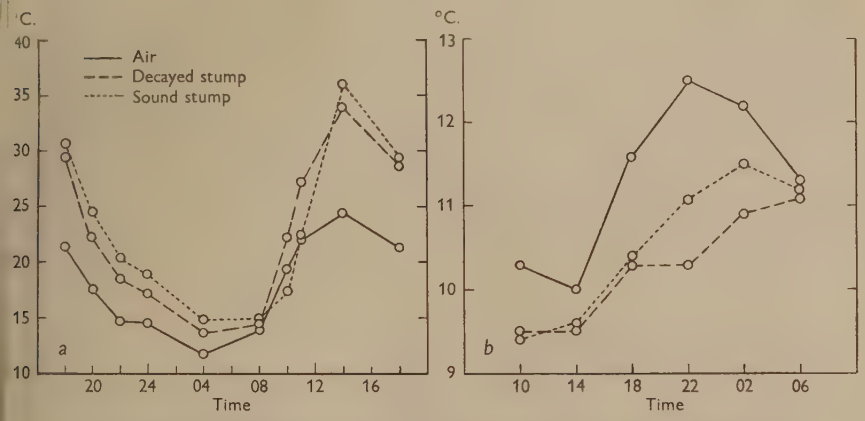

Fig. 2. Temperatures at soil level, in air and in a sound and in a decayed pine stump over 24 hr.: (*a*) 29–30 June 1951; (*b*) 26–27 June 1951.

t soil level are lower than those 20 cm. below the surface, at all times of the day. When ir temperatures are below 0° C., stump temperatures may not fall below this level. At oil level these findings agree with those of Savely (1939) on fallen logs and the ubsurface temperature variations in stumps agree with the findings of Baver (1948) ›n soil. The heat capacity of soils depends on their humus and water content. In ummer, stumps in sand reach higher temperatures than those in soil with a high umus content.

Temperature fluctuations in slightly decayed and highly decayed stumps are imilar, but the response to changes in temperature is more rapid in decayed wood Fig. 2*a*) which is characterized by a high water content. Temperature relations in ›ine stumps vary with the weather. During a cold wet period in summer, tempera- ures were recorded in stumps in the open (Fig. 2*b*). The conditions on these 2 days 26–27 June) are clearly different from those recorded 2 days later (Fig. 2*a*).

The temperature relations of pine stumps in clearings are very different from those n the forest, where there is shade and a pine needle blanket covers the forest floor.

Recordings of temperature taken in a stump in the forest and in a stump in the open and of the air in both localities show (Fig. 3) that forest temperatures fluctuate less than those in the clearings, and that whereas air temperatures are higher than stump temperatures in the forest, in the clearings stump temperatures are the highest. A sea mist which arose about 9.30 a.m. caused a drop in temperature.

The recordings in the field give a general indication of temperature relations in pine stumps. Diurnal and seasonal cycles occur, but these may be considerably modified by the nature of the soil, the degree of stump decay, the site of the stump and weather.

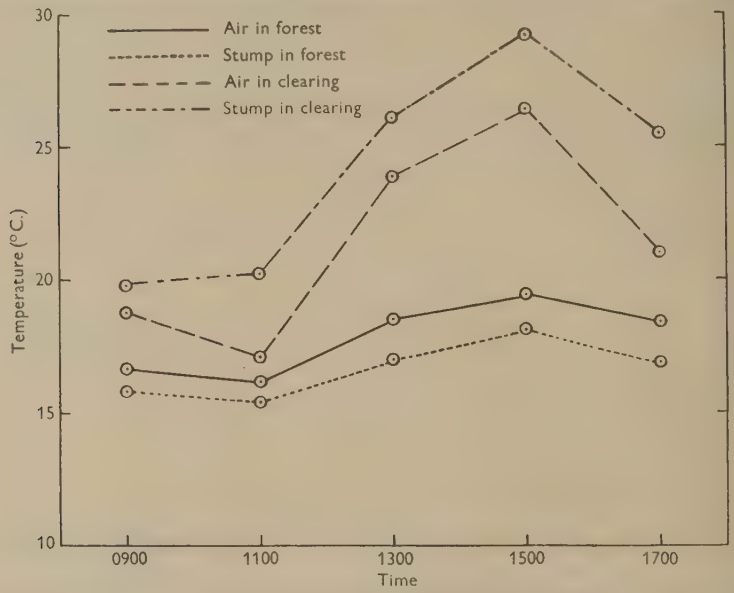

Fig. 3. Temperatures at soil level, in air and in pine stumps over an 8 hr. period, in a clearing and in the forest, 19 July 1951.

(*b*) *Moisture and decay*

Moisture content and fungal decay in pine stumps are interdependent. The effect of decay on the density and moisture content of wood has been studied by Findlay (1940), and Cartwright & Findlay (1946). Savely (1939) found that the moisture content in pine logs was seldom less than 50%, and values over 300% were common in highly decayed pine wood. In the decaying pine stumps at Formby, the lacunae formed by the action of the wood-rotting fungi become filled with water. When sufficient water is available to fill the airspaces, the moisture content of the wood rises and the bulk density decreases as decay progresses. In the clearings loss of water by evaporation is reduced to a minimum in the buried section of the stump. The moisture content of the free portion fluctuates considerably, except in the winter when the stump is saturated for most of the time. Stumps in the forest have a high moisture content throughout the year.

The relationship between the moisture content of wood and the relative humidity of cavities in the wood is not well known. Savely (1939) quotes data from Hawley & Wise

.926), and concludes that wood containing over 50% moisture will raise the humidity f a small enclosed airspace to the saturation point. Becker (1943) gives a table owing the relationship between percentage moisture content of wood and relative umidity, and it would appear that moisture contents over 28% will raise the relative umidity of cavities in the wood to 100%. Since the moisture contents recorded in ne present study were above 50%, except in stumps in exposed sites in the last phase f decay, it is reasonable to conclude that the galleries of the wood-boring insects in ine stumps almost always contain air which is saturated. The relationship between ne moisture content of the wood and larval growth would appear to be a useful line f research in further studies on xylophagous insects.

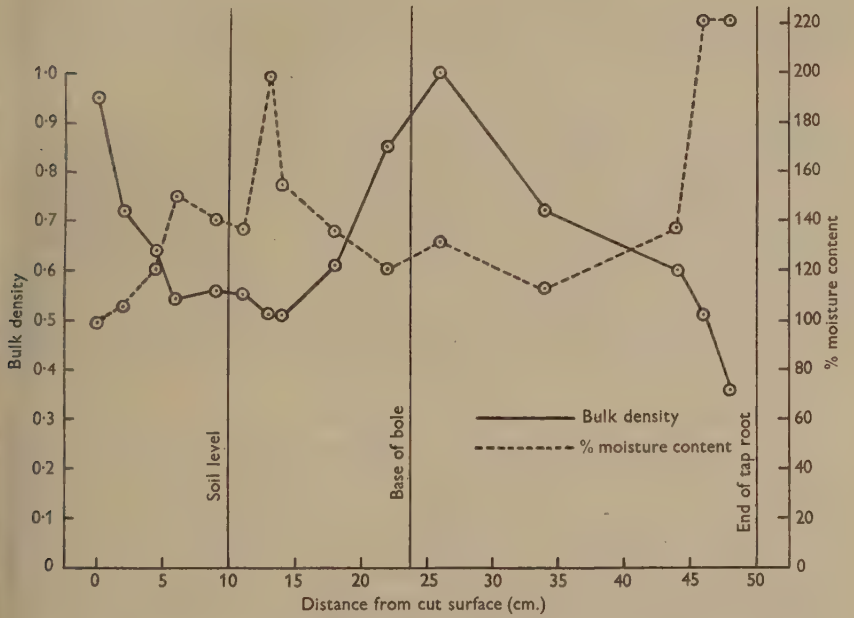

Fig. 4. Bulk density and percentage moisture content of the outer sapwood of a semi-decayed pine stump along its whole length.

Decay is very irregular in pine stumps. Large stumps take longer to decay than small ones, under comparable conditions (Derksen 1941). The same author noticed that the side of the stump facing south tends to be more decayed than the north side. Determinations of moisture and decay in the Formby area show that stumps which are inclined to the horizontal tend to be more decayed on the upper surface; vertical stumps on hillsides are most decayed on their uphill face.

In the early stages of decay individual stumps show little variation in bulk density of the wood; there is an increase in variability of bulk density and moisture content as decay progresses. In summer the moisture contents of highly decayed stumps vary from 20 to 400%, whilst in slightly decayed stumps it usually varies from 50 to 150%.

The distribution of fungal mycelia determines the course of decay. Temperature and moisture influence the growth of fungi in wood (Cartwright & Findlay 1934, Findlay 1940). Observations in the field indicate that fungi invade stumps chiefly via the roots and the bole a short distance from the top. In the laboratory moisture and bulk density determinations were made in a decayed stump by cutting wood samples from the outer sapwood along its whole length. This series of observations in one stump (Fig. 4) shows the general correlation between bulk density and moisture content for the outer sapwood in the various regions. The bulk density is relatively low and the moisture content relatively high, about soil level and at the end of the tap root. This suggests that decay has progressed from these two regions and supports the observations made in the field. In highly decayed stumps the only parts which contain any semblance of intact wood are the base of the bole and the cut surface. Derksen (1941) suggests that resins, exuded at the cut surface, prevent decay.

(*c*) *Types of decay and fungi involved*

A study was made of the fungi infesting pine stumps in the Formby district. *Tricholoma rutilans* (Schaeff.) Fr. and *Hypholoma fasciculare* (Huds.) Fr. are the most abundant and widely spread fungi and are undoubtedly the chief agents of decay. Both are saprophytic. *Tricholoma* was only found in stumps in the later stages of decay. Infested wood varies in colour from golden brown to dark brown, and it retains its shape until a very late stage. *Hypholoma* was observed in stumps in all phases of decay. The wood turns yellow and as decay progresses the colour fades and softening increases until a white stringy mass is produced. Weathered exposed regions often become dark brown.

Several fungi appear to be characteristic of stumps in an early phase of decay. *Armillaria mellea* (Vahl.) Quél. which gives rise to a white rot in wood is not common in the pine wood area; it probably persists until an advanced stage of decay. Wood infested by *Flammula sapinea* Fr. is brown in the later phases of decay. *Fomes annosus* Fr., a heart rot of standing trees, was found in several localities. *Polyporus stipticus* (Pers.) Fr. and *P. amorphus* Fr. occur in cracks on the cut surface and underneath the bark. *Polystictus abietinus* (Dicks.) Fr. occasionally infests the stumps.

All the stumps examined in the final stages of decay contained either a brown rot or a white rot. The relatively dry brown rotted woods retain their shape until a late stage, whilst the much moister white rotted woods shrink and lose their shape. The white and brown rots can be distinguished by the chemical processes involved in decay (Campbell 1930, 1931, 1932; Findlay 1940; Cartwright & Findlay 1943, 1946).

Some 200 stumps in all stages of decay were examined in the pine wood area. In clearings wood-rotting fungi showed a distinctly local distribution. Several cut-over areas were infested only by *Tricholoma* whilst others contained only *Hypholoma*. In areas where both fungi occur one is always clearly dominant. Colonies of *Fomes annosus*, *Polyporus amorphus* and *Flammula sapinea* were also found.

The observations suggest that some fungi show a preference for fairly sound stumps, others tend to occur mostly in highly decayed stumps, and certain fungi infest stumps in all conditions of decay. Bearing these points in mind, the following hypothesis for succession of wood-rotting fungi is suggested.

Succession from the living tree to the final decay of the stump may follow one of three courses. The living tree may be felled and its stump, which contains sound wood and is embedded in the soil, is then open to attack by saprophytic fungi. On the other hand, the tree may be parasitized by fungi whilst it is still living (*Armillaria mellea*, *Fomes annosus*) and so when felling takes place the stump will be initially decayed and saprophytic fungi will then consume the wood. If felling of the parasitized tree is delayed, then the saprophytic fungi may be present before felling. Sporophores of *Hypholoma fasciculare* have been observed on dead standing trees which were semi-decayed. Thus the stump at the felling of the tree may be in any state of decay. The saprophytic fungi may be either white or brown rots and so there is a bifurcation of the route of succession. The saprophytic fungi appear to fall into three groups; those which prefer fairly sound wood, those which prefer decayed wood and finally those which occur on wood humus (*Crepidotus nidulans* (Pers.) Quél. and *Lactarius rufus* Scop.) Fr.).

This picture is undoubtedly an over-simplification of the real state of affairs, but it roughly fits the known facts and serves as a useful approximation in the consideration of the relationships between the fungi and the insect populations of pine stumps. Findlay (1940) has described how a succession of fungi may occur during the decomposition of a log.

It is evident that fungi have an important effect on the physical and the chemical nature of the wood, and since different species of fungi give rise to characteristic types of decay, it is reasonable to suppose that they will play some part in determining the distribution of the insect communities in pine stumps. This aspect has been little studied in previous work on the ecology of wood-inhabiting insects.

(*d*) *The insect fauna*

The Coleoptera are the dominant order in pine stumps. Seventy species of beetles have been recorded, of which ten are known to be xylophagous, ten fungivorous, thirty-one predacious, one parasitic, and twenty-three either chance visitors or using the stump as a site for hibernation, nest building or pupation. The Diptera are represented by large numbers of Sciaridae and Mycetophilidae. The hymenopteran species are either xylophagous (*Urocerus gigas*), parasitic, or use the stumps as a nesting site. The Collembola occur in large numbers. Several Lepidoptera use stumps as a site for pupation, and at least one species is a fungus feeder. Species of Hemiptera, Psocoptera and Dermaptera are also recorded.

INSECT DISTRIBUTION

An estimation of the kinds and numbers of insects in particular habitats within pine stumps gives some idea of the most favourable conditions for some species. From an analysis of the field data in the species list (Appendix) some general conclusions can be drawn. Some species may occur in any stump whilst others appear to prefer those in either the forest or clearings. The distribution of the xylophagous coleoptera illustrates this. *Criocephalus ferus* occurs more abundantly in stumps in the clearings than in stumps in the forest, while the Scolytids show no preference. Counts of stumps, which were or had been inhabited by *Criocephalus* and the Scolytids, were

made in equal areas in the clearings, the forest verge and the depth of the forest. These three types of locality formed a continuous transect 10 m. wide, and the length of the transect in each locality was 15 m. Samples were taken from two such transects about a mile apart. The results are indicated in Fig. 5. The histogram demonstrates that in each transect the Scolytids attack almost all stumps both in the forest and clearings, but *Criocephalus* occurs mostly in the clearings where almost all the stumps contain the characteristic tunnels. There appears to be a gradient of distribution from the clearings to the forest for *Criocephalus*. *Hylobius abietis* shows a preference for stumps in the clearings but a large proportion of the forest stumps are also attacked. This observation supports Trägårdh's (1930) findings in Sweden.

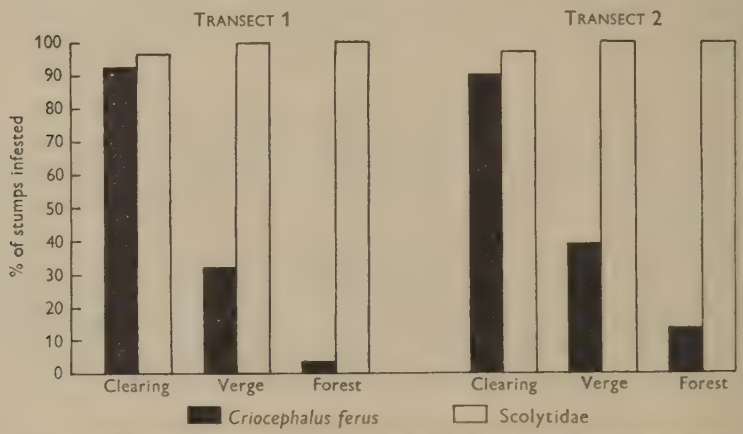

Fig. 5. Histograms showing the percentage of pine stumps infested by *Criocephalus ferus* and Scolytidae along two transects a mile apart, through clearing, forest verge and forest.

Several species of Coleoptera which feed on fungal mycelia under the bark and on the cut surface are most abundant in exposed sites. One exception, *Lordithon trinotatus*, has a preference for forest stumps. Sciarid larvae occur in large numbers in stumps in clearings; they are less common in the forest.

Decay, moisture and temperature are probably the most important physical factors which affect the insect distribution. Although these variables are closely interdependent, it is possible to elucidate some of the broader associations. In many cases the presence of a species is associated with the phase of stump decay (see p. 156):

Phase I. The Scolytidae and Curculionidae are restricted to this phase. Many beetles which feed on fungal mycelia or the sporophores occur in large numbers. Three species of *Rhizophagus* and some small Staphylinids form large aggregations in the tunnels made by the Scolytids.

Phase II. The sapwood-feeding Coleoptera are chiefly associated with this phase. The Collembola, Ceroplatinae and the fungus-feeding larvae of the moth *Esperia sulphurella* reach their optimum numbers. Several predacious species also occur—*Staphylinus ater*, *Phyllodrepa grandiloqua* and *Tachypeza nubila*. The Cecidomyiid *Pezomyia vanderwulpi*, which inhabits the subcortical region, is also very abundant.

Phase III. A large number of Carabidae, Staphylinidae, fungus-feeding Diptera nd Coleoptera, and many others are associated with this phase. The Aculeate ymenoptera are most prevalent and *Forficula auricularia*, *Hallomenus binotatus* and ne larvae of various Elateridae and Diptera are common in the decayed wood.

In the white rotted wood the chief inhabitants are *Neanura muscorum* and Sciarid rvae. In brown rot stumps the larvae of *Mycetophila fungorum*, *Bolitophila cinerea*, *Xechia separata*, *Thereva bipunctata* and *Melanotus rufipes* are characteristic. It is oncluded that the effect of decay on the wood is a major factor governing insect istribution. In many cases it is the nature of the physical environment associated ith the type of fungus, rather than the fungus itself which is so important.

The Collembola occur in large numbers in very decayed stumps with a high moisture ontent. In exposed sites they may be confined to damp parts below soil level, but in ne forest the whole stump may be inhabited throughout the whole year. Some species f Collembola (unidentified) appear to require free water. When they are placed on aturated wood in a container along with Sciarid larvae, the Sciarids collect on the amp surface of the wood, whilst the Collembola congregate at the base where free vater still remains. Larvae of the Sciarid *Plastosciara pernitida*, reared on decayed vood containing a large amount of free water, died within 7–10 days.

The larvae of *Criocephalus ferus* are sensitive to changes in moisture content of the vood. In summer they do not often occur above soil level in highly decayed stumps, nd this distribution is not entirely due to the high temperatures in the wood, nor to he advanced state of decay, since similar conditions exist just below soil level, except hat the moisture content is higher. Larvae of *C. ferus* were placed in glass tubes, 2 ft. ong and $\frac{3}{4}$ in. in diameter, closed at both ends and filled with pulverized decayed wood anging in moisture content from 10% at one end to 350% at the other. The tubes vere placed horizontally. Larvae introduced at both ends of the tubes congregated t the moist end in 2 days.

Larvae of *Hallomenus binotatus* will only grow and metamorphose in moist wood 80–150% moisture content). Some species, especially those associated with sand lunes, prefer dry conditions; for example, the solitary bees and wasps, the three pecies of *Calathus*, *Phylan gibbus* and *Philopedon plagiatus*. Larvae of *Thereva ipunctata* can complete their life cycle in relatively dry wood (50% moisture content).

Temperature gradients in pine stumps appear to influence the distribution of some nsects. In decayed stumps the larvae of Carabidae, *T. bipunctata*, *Dysmachus trigonus*, *Lasiopogon cinctus* and *Melanotus rufipes* occur mostly in the wood below soil level luring the winter, whilst in the summer they frequently appear at the cut surface of he stump. This seasonal distribution of larvae is more evident in *Criocephalus ferus*. All the larvae were removed from two stumps, one in February and the other in the ollowing June. There were 134 larvae in the base and roots, and fifty-seven at the top f the stump in the February count. The stump examined in June had twenty-nine arvae in the base and roots and forty-nine at the top. If the figures are arranged in the orm of a contingency table, then $\chi^2 = 25{\cdot}07$ and $P < 0{\cdot}01$, suggesting that there is an ssociation between location in the stump and season. The results support field bservations that the larvae tend to migrate downwards in autumn and upwards in pring. The observations suggest that this seasonal migration may be associated with

the reversal of the temperature gradients in the stumps in autumn and spring (see p. 156). Dowdy (1944) has described the influence of temperature on the vertical migrations of soil-inhabiting invertebrates at different times of the year. It seems likely that similar migrations occur in some species in stumps.

In general the fauna of stumps in clearings is richer in species than the fauna of forest stumps. As decay progresses the stumps in the clearings are inhabited by an increasing number of species, the number of xylophagous species decreasing and the numbers of fungivorous species increasing. In the final stages of decay the insect fauna of stumps containing a brown rot is richer in species than the fauna of white rot stumps.

Table 1. *The dominant insects characteristic of each phase of decay in clearings and forest*

	All sites	
PHASE I	*Hylastes ater*	*Rhizophagus depressus*
	Hylurgops palliatus	*R. dispar*
	Myelophilus pinniperda	*R. ferrugineus*
	Hylobius abietis	*Phloeonomus pusillus*
	Pissodes castaneus	*Phloeopora testacea*

	Clearing		Forest
	Bare sand dune	Sand dune colonized by *Carex arenaria*	
PHASE II			
	Criocephalus ferus	*Criocephalus ferus*	Collembola spp.
	Philopedon plagiatus	*Epuraea pusilla*	*Ernobius mollis*
	Phylan gibbus	*Esperia sulphurella*	*Lordithon trinotatus*
	Melanimon tibialis	*Glischrochilus quadripunctatus*	*Soronia grisea*
	Calathus mollis	*Dromius quadrinotatus*	*Metabletus foveatus*
	C. erratus	*Ceroplatinid larvae*	*Notiophilus substriatus*
	C. melanocephalus		*Pezomyia vanderwulpi*
PHASE III			
	Criocephalus ferus	*Criocephalus ferus*	Collembola spp.
	Melanotus rufipes	*Quedius tristis*	*Mycetophila luctuosa*
	Lasius niger	*Q. xanthopus*	*Xantholinus linearis*
	Myrmica laevinodis	*Catops tristis*	*Hallomenus binotatus*
	M. scabrinodis	*Limonius aeruginosus*	
	Coelocrabro leucostomoides	*Neanura muscorum*	
	C. ambiguus	*Staphylinus olens*	
	Solenius continuus	*Thereva bipunctata*	
	Megachile maritima	*Mycetophila fungorum*	
	M. versicolor	*Bolitophila cinerea*	
	Osmia coerulescens	*Exechia separata*	
	Ammophila sabulosa	*Plastosciara pernitida*	
		P. schineri	

INSECT SUCCESSION

The pine stumps occur in three general sites: clearings with stable sand dune, clearings with sand dune in the process of plant colonization, and forest. Insect succession has been studied in stumps in each type of locality. In stumps which are initially decayed the early stages of succession may be passed before felling. The insects which invade the pine stumps immediately after felling are the same whatever the locality. The Scolytidae and Curculionidae which attack the cambium exposed at

he cut surface, are the first colonizers; they are closely followed by their parasites and predators. At a later stage of decay variations in insect succession occur which differentiate the populations characteristic of clearings and forest.

Table 2. *The insect fauna of a slightly decayed (Phase I) and a highly decayed (Phase III) pine stump*

(*F*=fungus-feeder; *X*=xylophagous; *P*=predator; *Pa*=parasite.)

	Numbers	Feeding habits
PHASE I		
COLLEMBOLA		
Neanura muscorum	96	*F*
Collembola spp. (unidentified)	30	*F*
COLEOPTERA		
Epuraea pusilla	1	*F*
Hylastes ater adults	20	*X*
Hylobius abietis larvae	11	*X*
Hylurgops palliatus adults	126	*X*
Leistus spinibarbis adults	1	*P*
Nebria salina adults	3	*P*
Phloeonomus pusillus adults	27	*F*
Phloeopora testacea adults	5	*Pa*
Phylan gibbus adults	1	*P*
Rhizophagus depressus adults	35	*P*
R. dispar adults	12	*P*
R. ferrugineus adults	6	*P*
Scolytid larvae	*c.* 500	*X*
DIPTERA		
Plastosciara pernitida larvae	30	*F*
Pezomyia vanderwulpi larvae	32	*F*
Tachypeza nubila adults	3	*P*
Total	939	
PHASE III		
COLLEMBOLA		
Neanura muscorum	*c.* 150	*F*
COLEOPTERA		
Calathus erratus adults	4	*P*
C. melanocephalus adults	1	*P*
Criocephalus ferus larvae	11	*X*
DIPTERA		
Ceroplatinae larvae	12	*P*
Plastosciara pernitida larvae	*c.* 5500	*F*
Total	5678	

In the clearings as the cambium is consumed the Scolytid and Curculionid populations wane and the numbers of *Criocephalus* larvae greatly increase. Fungus-feeders collect under the bark and in the galleries of the wood-boring beetles. With the destruction of the cambium the subcortical gap widens and insects from the surrounding environment invade this microhabitat. Stumps on bare sand dunes are colonized by insects usually associated with dry conditions and a sand dune environment. Ants, carpenter bees, digger wasps and sand wasps are abundant. Stumps surrounded by a dense mat of *Carex arenaria* are invaded by insects such as Sciaridae and Mycetophilidae which favour moist conditions.

In the forest the decrease in the numbers of cambium feeders is rarely followed by an increase in the numbers of *Criocephalus* larvae, which only occur in about 5% of the

stumps. Usually the only xylophagous form inhabiting the semi-decayed stumps is *Ernobius mollis*, but it is not an important destructive agent. Fungivorous beetles occur on the sporophores of the polypores which cover the cut surface. Eventually insects associated with the duff stratum of the forest floor invade the subcortical gap. Numerically springtails, which are very common on the forest floor, dominate the stump fauna. They enter the stump as soon as a space is formed beneath the bark and persist until the final stages of decay. The dominant insects characteristic of each phase of decay in the various sites are listed in Table 1.

INSECT NUMBERS AND FOOD RELATIONS

The insect populations of a pine stump in Phase I of decay and one in Phase III were analysed and counted on 15 May 1952 (Table 2). In the Phase I stump of the 939 insects counted 657 were xylophagous, 216 fungivorous, 61 predatory and 5 parasitic. In the Phase III stump a total population of 5678 insects was estimated, of which 5650 were fungivorous, 11 xylophagous, 17 predatory and none parasitic. In Phase I stumps the xylophagous forms are the dominant insects and in Phase III the fungus-feeding insects are dominant. In both stumps the predatory and parasitic forms are relatively few in relation to the xylophagous and fungivorous forms. The largest population occurs in the Phase III stump. Counts of insects in the parasite-predator, fungus-feeding and xylophagous groups show that a pyramid of numbers exists (Fig. 6). The counts demonstrate the more general observations in the field.

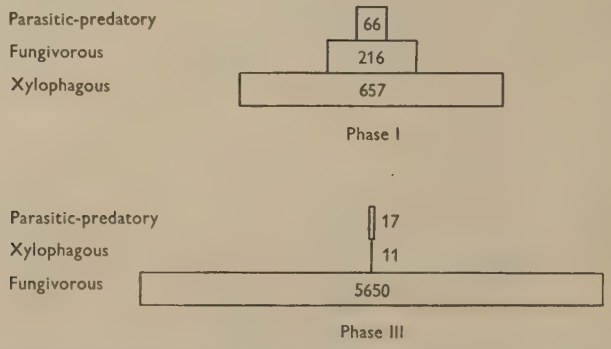

Fig. 6. The food relations and pyramid of numbers of insects inhabiting a slightly decayed (Phase I) and a highly decayed (Phase III) pine stump. The number of individuals in each of the feeding groups is indicated.

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SUMMARY

1. Temperature fluctuations in stumps at soil level resemble those in fallen logs; in the buried part they resemble those of the soil. Changes in external temperature are more rapidly reflected in the wood as decay progresses. Temperatures fluctuate less in forest stumps than in those in the clearings. Stumps in the sand reach higher temperatures than those in soil of high humus content.

2. As the wood decays the bulk density decreases and the moisture content increases. Since the moisture content of stumps is generally above 50%, the air in the galleries of wood-boring beetles is probably almost always saturated.

3. Fungi chiefly invade the stumps via the roots and the bole about soil level.

4. In the clearings *Criocephalus ferus* Muls. (Coleoptera: Cerambycidae) and the fungi *Tricholoma rutilans* and *Hypholoma fasciculare* are the principal agents of stump destruction; in the forest the fungi alone are concerned.

5. A total of 133 insect species was collected from stumps in all phases of decay. Beetles dominate the fauna.

6. The distribution of the insect fauna is influenced by the site of the stump, phase of decay and the type of wood-rotting fungus (brown or white rot).

7. As decay progresses the total number of species increases, the number of xylophagous species decreases and the fungus-feeders increase. Most species favour wood with a high moisture content; others, especially those associated with sand dunes, prefer drier conditions.

8. A succession of insects occurs as pine stumps decay, well defined in clearings but not clear-cut in the forest.

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* Original not consulted.

APPENDIX

Insect species collected from pine stumps in the Formby district from August 1950 to September 1952

The insect nomenclature is based on Kloet & Hincks (1945). The feeding habits are given where they are known and general notes on the biology and habitat. The abundance of the species is expressed in five categories, based on the numbers caught.

Key

Feeding habits—*X* = xylophagous; *F* = fungivorous; *Pa* = parasitic; *Pr* = predatory.
State of stump decay—I, slightly decayed; II, semi-decayed; III, highly decayed.
Abundance—VC = very common, > 1000 specimens; C = common, 100–1000; A = abundant, 20–100; O = occasional, 2–20; R = rare, one specimen; — = not recorded.
Notes—H = hibernating; Ch = chance visitor; Pu = pupating.

	Family	Feeding habits	Phase of stump decay	Abundance in Clearings	Abundance in Forest	Notes
COLLEMBOLA						
Neanura muscorum (Temp.)	Neanuridae	*F*	III	VC	VC	.
Orchesella cincta (L.)	Mydoniidae	.	II	R	—	.
Collembola spp.		*F*	II, III	VC	VC	.
DERMAPTERA						
Forficula auricularia L.	Forficulidae	*Pr*	III	C	—	.
PSOCOPTERA						
Mesopsocus immunis (Steph.)	Mesopsocidae	*F*	I	A	—	.
M. unipunctatus (Muell.)	Mesopsocidae	*F*	I	A	—	.
HEMIPTERA						
Anthocoris sp.	Anthocoridae	.	III	R	—	.
Coranus subapterus (Deg.)	Reduviidae	*Pr*	III	A	—	.
Heterogaster urticae (Fab.)	Lygaeidae	.	III	A	—	.
Trapezonotus arenarius (L.)	Lygaeidae	.	III	A	—	.
LEPIDOPTERA						
Bupalus piniarius (L.)	Selidosemidae	.	II, III	—	A	Pu
Celaena secalis (L.)	Caradrinidae	.	III	O	—	Pu
Dioryctria abietella (Sch.)	Phycitidae	.	II, III	—	A	Pu
Esperia sulphurella (Fab.)	Oecophoridae	*F*	II	C	—	.
Hypocrita jacobaeae (L.)	Arctiidae	.	III	C	R	Pu
Phthorimaea sp.	Gelechiidae	.	III	VC	—	Pu
COLEOPTERA						
Adonia variegata (Goeze)	Coccinellidae	*Pr*	II, III	O	O	H
Amara aenea (Degeer)	Carabidae	.	III	O	—	Ch
A. familiaris (Duft.)	Carabidae	.	III	O	—	Ch
A. lucida (Duft.)	Carabidae	.	III	O	—	Ch
Anatis ocellata (L.)	Coccinellidae	*Pr*	I, II	O	A	H
Anisotoma humeralis (Fab.)	Leiodidae	*F*	I, II	A	—	.
Apion ononis Kirby	Curculionidae	.	II	O	R	Ch
Asemum striatum (L.)	Cerambycidae	*X*	II	O	—	Local
Bembidion quadrimaculatum (L.)	Carabidae	.	III	R	—	Ch
Bradycellus harpalinus (Serv.)	Carabidae	*Pr*	II	O	—	.
Calathus erratus Sahl.	Carabidae	*Pr*	II, III	VC	O	H
C. melanocephalus (L.)	Carabidae	*Pr*	II, III	A	O	H
C. mollis (Marsham)	Carabidae	*Pr*	II, III	C	O	H
Catops tristis (Panzer)	Silphidae	.	II	O	—	Sap feeder
Coccinella septempunctata L.	Coccinellidae	*Pr*	II	A	C	H
Conosomus testaceus (Fab.)	Staphylinidae	*Pr*	II, III	O	R	.
Criocephalus ferus Muls.	Cerambycidae	*X*	I, II, III	VC	C	.

	Family	Feeding habits	Phase of stump decay	Abundance in Clearings	Abundance in Forest	Notes
COELOPTERA (*continued*)						
Crioceris asparagi (L.)	Chrysomelidae	.	II, III	C	O	H
Dermestes peruvianus Castelnau	Dermestidae	.	III	R	–	Ch
Dromius quadrinotatus (Panzer)	Carabidae	*Pr*	II	C	R	.
Epuraea pusilla (Illiger)	Nitidulidae	*F*	II, III	C	A	.
Ernobius mollis (L.)	Anobiidae	*X*	II	–	VC	Local
Glischrochilus quadri-punctatus (L.)	Nitidulidae	*F*	I, II	C	–	.
Gonodera luperus (Herbst)	Alleculidae	*Pr*	III	O	–	.
Hallomenus binotatus (Quensel)	Serropalpidae	*F, X*	III	VC	VC	.
Halyzia sexdecimguttata (L.)	Coccinellidae	*Pr*	II, III	O	A	H
Harpalus anxius (Duft.)	Carabidae	*Pr*	III	C	–	.
H. neglectus Serv.	Carabidae	*Pr*	III	C	R	.
Hylastes ater (Paykull)	Scolytidae	*X*	I	VC	VC	.
Hylobius abietis (L.)	Curculionidae	*X*	I	VC	C	.
Hylurgops palliatus (Gyllenhal)	Scolytidae	*X*	I	VC	VC	.
Lathridius nodifer Westwood	Lathridiidae	.	III	R	–	.
Leistus ferrugineus (L.)	Carabidae	*Pr*	III	C	–	H
L. spinibarbis (Fab.)	Carabidae	*Pr*	I, II, III	C	–	H
Limonius aeruginosus (Olivier)	Elateridae	.	II	C	–	From *Carex*
Longitarsus jacobaeae (Waterhouse)	Chrysomelidae	.	II	O	–	Ch
Lordithon trinotatus (Erichson)	Staphylinidae	*F*	I, II	A	C	H
Melanimon tibialis (Fab.)	Tenebrionidae	.	II, III	C	O	.
Melanotus rufipes (Herbst)	Elateridae	*X, F*	III	A	O	.
Metabletus foveatus (Geoffroy in Fourcroy)	Carabidae	*Pr*	II	C	A	.
Mycetoporus brunneus (Marsham)	Staphylinidae	*Pr*	II	A	–	.
Myelophilus pinniperda (L.)	Scolytidae	*X*	I	VC	VC	.
Nebria degenerata Schauf.	Carabidae	*Pr*	III	O	–	.
Notiophilus aquaticus (L.)	Carabidae	*Pr*	III	R	–	Ch
N. substriatus Waterhouse	Carabidae	*Pr*	I, II, III	O	O	.
Omalium rivulare (Paykull)	Staphylinidae	*Pr*	II	A	R	.
Otiorrhynchus ovatus (L.)	Curculionidae	.	I, II	C	C	Sap feeder
Philopedon plagiatus (Schaller)	Curculionidae	.	I, II	C	A	Sap feeder
Phloeonomus pusillus (Gravenhorst)	Staphylinidae	*F*	I	C	C	.
Phloeopora testacea (Mannerheim)	Staphylinidae	*Pa*	I	A	A	Host scolytids
Phylan gibbus (Fab.)	Tenebrionidae	.	II, III	VC	O	.
Phyllodrepa grandiloqua Luze	Staphylinidae	*F*	I, II	–	O	.
Pissodes castaneus (Deg.)	Curculionidae	*X*	I	C	A	.
Quedius tristis (Grav.)	Staphylinidae	*Pr*	II, III	A	–	.
Q. xanthopus Erichson	Staphylinidae	*Pr*	II	O	–	.
Rhagonycha fulva (Scopoli)	Cantharidae	.	II	O	–	Ch
Rhizophagus depressus (Fab.)	Rhizophagidae	*Pr*	I	VC	VC	.
R. dispar (Pay.)	Rhizophagidae	*Pr*	I	VC	VC	.
R. ferrugineus (Pay.)	Rhizophagidae	*Pr*	I	VC	VC	.
Simplocaria semistriata (Fab.)	Byrrhidae	*F*	I, II	A	–	.
Soronia grisea (L.)	Nitidulidae	*F*	I, II	R	A	.
Staphylinus ater Grav.	Staphylinidae	*Pr*	II, III	C	O	.
S. brunnipes Fab.	Staphylinidae	*Pr*	III	A	O	Near *Carex*
S. olens Muell.	Staphylinidae	*Pr*	III	O	–	Near *Carex*
S. stercorarius Olivier	Staphylinidae	*Pr*	III	O	–	Near *Carex*
Strophosomus melanogrammus (Forst.)	Curculionidae	.	II	–	R	Ch
Thanasimus formicarius (L.)	Cleridae	.	III	R	–	Pu, Ch
Thanatophilus rugosus (L.)	Silphidae	.	III	R	–	Pu, Ch
Trechus obtusus Erich.	Carabidae	.	III	R	–	Ch
Xantholinus linearis (Olivier)	Staphylinidae	*Pr*	II, III	R	O	.

	Family	Feeding habits	Phase of stump decay	Abundance in Clearings	Abundance in Forest	Notes
HYMENOPTERA						
Ammophila sabulosa (L.)	Sphecidae	*Pr*	III	C	–	H
Apanteles popularis (Haliday)	Braconidae	*Pa*	III	A	–	Host *Hypocrita jacobaeae*
Coelocrabro ambiguus (Dahlbom)	Sphecidae	*Pr*	III	A	–	Nesting
C. leucostomoides Richards	Sphecidae	*Pr*	III	A	–	Nesting
Cratichneumon nigritarius (Grav.)	Ichneumonidae	*Pa*	III	–	O	.
Enicospilus sp.	Ichneumonidae	*Pa*	III	O	–	.
Habritys brevicornis (Ratzeburg)	Lamprotatidae	*Pa*	III	VC	–	Host *Hypocrita jacobaeae*
Lasius niger (L.)	Formicidae	*Pr*	III	VC	–	.
Megachile maritima (Kirby)	Apidae	*Pr*	III	A	–	Nesting
M. versicolor Smith	Apidae	*Pr*	III	A	–	Nesting
Melanichneumon perscrutator (Wesmael)	Ichneumonidae	*Pa*	III	C	–	Host *Hypocrita jacobaeae*
Meteorus obfuscatus (Nees)	Braconidae	*Pa*	III	C	C	Host *Hallomenus binotatus*
Myrmica laevinodis Nylander	Formicidae	*Pr*	III	VC	–	.
M. scrabrinodis Nylander	Formicidae	*Pr*	III	VC	–	.
Ophion sp.	Ichneumonidae	*Pa*	III	O	–	.
Osmia coerulescens (L.)	Apidae	*Pr*	III	A	–	Nesting
Phygadeuon sp.	Ichneumonidae	*Pa*	III	–	R	.
Solenius continuus (Fab.)	Sphecidae	*Pr*	III	A	–	Nesting
Urocerus gigas (L.)	Siricidae	*X*	I	R	–	.
Vespula germanica (Fab.)	Vespidae	*Pr*	III	C	–	H and nesting
V. vulgaris (L.)	Vespidae	*Pr*	III	C	–	H and nesting
DIPTERA						
Anthomyiidae sp.	.	.	III	–	O	.
Bibio leucopterus (Meigen)	Bibionidae	*Pr*	III	R	–	Ch
Bolitophila cinerea Meigen	Mycetophilidae	*F*	III	C	–	.
Calliphora erythrocephala (Meigen)	Calliphoridae	.	III	O	O	.
Carcelia gnava (Meigen)	Larvaevoridae	*Pa*	III	O	–	.
Ceroplatinae sp.	Mycetophilidae	*Pr*	II, III	C	A	.
Clusiodes gentilis (Collin)	Clusiidae	.	III	A	A	.
Dysmachus trigonus (Meigen)	Asilidae	*Pr*	III	O	–	.
Exechia separata Lundstroem	Mycetophilidae	*F*	II, III	–	A	.
Fausta vivida (Zetterstedt)	Larvaevoridae	.	III	O	–	.
Lasiopogon cinctus (Fab.)	Asilidae	*Pr*	III	O	–	.
Lonchoptera lutea Panzer	Lonchopteridae	.	III	–	O	.
Medeterus sp.	Dolichopodidae	*Pr*	III	A	O	.
Metopia argyrocephala (Meigen)	Calliphoridae	.	III	O	O	.
Mycetophila fungorum (Deg.)	Mycetophilidae	*F*	III	VC	VC	.
M. luctuosa Meigen	Mycetophilidae	*F*	II, III	A	VC	.
Nephrotoma submaculosa Edwards	Tipulidae	.	III	R	–	Ch
Pezomyia vanderwulpi (de Meijere)	Cecidomyiidae	*F*	II, III	O	VC	.
Philonicus albiceps (Meigen)	Asilidae	*Pr*	III	O	–	.
Plastosciara pernitida Edwards	Sciaridae	*F*	II, III	VC	VC	.
P. schineri Winnertz	Sciaridae	*F*	II, III	VC	VC	.
Sphixapata conica (Fallén)	Calliphoridae	*Pa*	III	O	–	Host *Megachile* spp.
Tachypeza nubila (Meigen)	Empididae	*Pr*	I, II	C	C	.
Thereva bipunctata Meigen	Therevidae	*Pr*	III	A	–	.
T. nobilitata (Fab.)	Therevidae	*Pr*	III	A	–	.
Trichocera saltator (Harris)	Trichoceridae	*F*	III	A	–	.

REVIEWS

THE FAUNA OF BRITAIN

B. P. Beirne (1952). *The Origin and History of the British Fauna.* Pp. x + 164; 60 text-figures. London: Methuen. Price 18*s*.

It seems to be generally accepted that there were four glaciations during the Ice Age, and, according to Dr Beirne, the last one oscillated so that there were three glacial phases and two relatively warm interglacial phases. With each advance and retreat of the ice the fauna of Europe withdrew and then spread north again, the various components becoming mixed up, with isolations here and exterminations there, to form an omelette, attempts to unscramble which are a source of continual fascination to-day. To a ringside observer, such as the reviewer, who has read some of the biological work but not the basic geological and geographical studies, the number of unknown factors seems to justify a sceptical attitude towards all attempts at unscrambling. For example, Beirne states categorically (p. 45) that there was a land connexion between Britain and Ireland early in the postglacial period, and Ford (1945, *Butterflies*, New Naturalist, no. 1) finds it impossible to suppose that the two countries could have been connected in a warm time later than the last interglacial period (p. 309). There appear to be no data about what the climate was like in areas that were free of ice during glacial periods. Britain was bigger then, much sea water being locked up as ice, and a great part of Beirne's case depends on some of the marginal areas having been warm enough for interglacial phase invaders to have survived on them, though on p. 147 he admits that there is no evidence that they were; to Matthews (1952, *British Mammals*, New Naturalist, no. 21) this suggestion 'is not entirely acceptable' (p. 376). Finally, there is the dispute about how long must elapse before isolation leads to differentiation, a controversy referred to again later. Beirne believes that it is not possible to trace the history of any species further back than the last glaciation, but he does attempt to divide the fauna into six categories according to whether they entered the country during the first, second, or third glacial phase, the first or second interglacial phase, or the postglacial period. Chapter 3, in which the different kinds of evidence are discussed and the various assumptions demanded set down, is the key chapter to the book.

There are five types of evidence. The first is palaeontological, and this is dismissed as of little value owing to the fragmentary nature of the fossil record of most animals. The second, historical evidence, is also passed over as too incomplete to be important, but this does not seem to the reviewer to be justified, because the ranges of some species have now been known sufficiently well for a century or more to show that there may be in that period changes which should make anyone hesitate before relating present-day range to events of thousands of years ago. Downes (1948, *J. Anim. Ecol.* **17**, 131–8), in a paper not referred to in this book, describes such changes in the ranges of certain butterflies and brings the structure of one of Beirne's earlier papers toppling to the ground. Thirdly comes ecological evidence, obviously of supreme importance. Any study of the history of the British fauna is really a study of species with a restricted distribution but there is the difficulty, recognized by Beirne, that the factors operating to limit the range of a species have rarely been analysed exactly and therefore how far most cases of restricted range are due to ecological requirements and how far to past history is difficult to determine. 'The chief objection', writes Dr Beirne in a passage that calls for no comment, 'to using ecological evidence is that it assumes that a species has not changed its ecological requirements since the ancestors of its existing population first invaded the British Isles. This is a reasonably safe assumption in most instances.' Fourthly there is taxonomic evidence, the argument being that the existence of subspecies indicates long isolation. Harrison Matthews (p. 376), discussing this question, points out that the pygmy shrew is our oldest species judging from the fact that it occurs all over Ireland, and the common and water shrews came in later, since they do not occur in Ireland; yet it is the pygmy shrew that is identical with the continental species and the other two that are subspecifically distinct. Both he and Beirne mention the St Kilda mouse, which became a subspecies within historic times. Thienemann (1950, 'Verbreitungsgeschichte der Süsswassertierwelt Europas', *Binnengewässer*, **18**) describes how a population of *Coregonus* introduced into a lake had become distinct from the

arent stock in 40 years or about seven generations (p. 573). Finally there is zoogeographical vidence. Much of Beirne's thesis hangs on the assumption that restricted range to-day ıdicates that the species sought refuge during unfavourable periods in a region adjoining that 'hich it now inhabits; for example, fen species survived a glacial phase on the land that is ow the Dogger Bank. This presupposes an immobility which seems improbable; the British sles are so small zoogeographically. Dr Beirne is aware of the objections, and points out that ıe evidence from any one of these sources alone is not of much account, and only when the vidence under all three heads tallies can a reasonably certain deduction be drawn.

Chapter 4 is about the Ice Age and the rest of the book, two-thirds of it, is devoted to the etails of the author's thesis. I think it is fair to take one example to illustrate his method. During the first glacial phase, he argues, the European hare became split into two groups, ıne adapted to cold conditions and one not, these being the ancestors of *Lepus timidus* nd *L. europeus* respectively. During the first interglacial phase *L. timidus* entered Britain. During the second glacial phase part of the population survived in the Celtic Land, that is the Atlantic coast, and ultimately gave rise to *L. hibernicus* (*L. timidus hibernicus* of Matthews) vhich inhabits Ireland to-day. In the second interglacial period the rest of the *L. timidus* ›opulation returned from the south and became isolated in Scotland to give rise to the present-lay *L. scoticus* (*L. t. scoticus* of Matthews). *L. europeus* also entered Britain during the second nterglacial phase and survived there the last glacial phase, which was a mild one. A simpler explanation would be that arctic and temperate species of *Lepus* arose at some time and by ;ome means that cannot be specified exactly, that the two advanced northwards into Britain ıfter the last retreat of the ice, and that the arctic species, finally confined to the north by competition with *L. europeus*, became isolated when Ireland and Scotland separated and gave rise to the two subspecies. *L. europeus*, advancing behind them, did not reach Scotland before the bridge to Ireland had broken. Beirne's objection to this theory, and the basis of his own elaborate one, is that it does not allow enough time for the formation of the species and sub-species; the British *L. europeus* is subspecifically distinct and must therefore have been isolated from the continental population for longer than the postglacial period. But how the two were kept apart, if, as is generally agreed, England was attached to the continent till well on into the postglacial, is not explained. Moreover why, if *Lepus europeus* was in Britain as early as Beirne postulates, it did not reach Ireland is not made clear, though its occurrence in the Hebrides (recent introduction according to Matthews) is brought forward as evidence that it was widespread in the last interglacial phase. The other refuge areas are the Cambrian Land, which is now beneath the Irish Sea, the Channel Land, and the Dogger Land.

This book contains a commendably large number of distribution maps, though it is exasperating that none includes more than the British Isles. Probably having been written too soon, it makes no reference to Thienemann's voluminous work, which is much to be regretted, because, both on account of the mass of material brought together and the scholarly treatment of it, writers on zoogeography will find it indispensable for many decades to come. Those who enjoy theorizing in realms where they are not tied down too much by hard facts will find Dr Beirne's book entertaining, but the teacher and the student who want an impartial survey of the field are advised to avoid it; they cannot do better than read chapter 13 in Harrison Matthews's *British Mammals*.

T. T. MACAN

THE HISTORY OF THE BISON

Frank Gilbert Roe (1951). *The North American Buffalo: A Critical Study of the Species in Its Wild State.* Pp. viii + 957. Toronto: University of Toronto Press; London: Geoffrey Cumberlege. Price 90*s*.

With the publication of this book, the history of the North American bison (which Dr Roe, 'following weighty precedent', prefers to call buffalo) may finally be regarded as a tale that is told. It is a fittingly monumental memorial to a monumental beast, extinct over nearly the whole of its once vast range. Dr Roe deals with every aspect of his theme as a historian—he describes himself as 'a layman in biology'—carefully quoting, comparing and analysing the numerous (often conflicting) accounts scattered through the records left by early settlers, hunters, explorers and Jesuit priests; as well as the later voluminous literature devoted solely to the history and habits of the species. This approach is the only one now possible to many

of the problems involved; and though 'One might very easily have observed the living species at Wainwright, prior to the closing of the Park... I share the opinion expressed by eminent zoologists' (though not by all of them) 'that a wild race are really living unnaturally under such conditions'.

While making full use, and recognizing the value, of the classical writings of Joel A. Allen, W. T. Hornaday, and Ernest Thompson Seton, whom he describes as the three serious historical generalizers on the buffalo, he disagrees with the first on some and the last two on many points, and supplies chapter and verse in each case for his dissent. Notable in this connexion, from the zoological standpoint, is his rejection of the idea, strongly supported by Hornaday, of regular northward and southward seasonal migrations (as apart from irregular movements) of the bison; and, from the sociological standpoint, his criticisms of the typical nineteenth-century view, again favoured by Hornaday, that improvidence and wasteful exploitation on the part of the Indians (even if these epithets are admissible as descriptive of the Indian mentality) contributed to any considerable extent to the disappearance of the animal.

The book is indeed largely an anthropological study as well as a study of an ungulate species. One of the chapters is entitled 'The Influence of the Buffalo Environment upon Indian Mentality', and the author remarks: 'I know of no other instance throughout the entire world wherein from one single source so many commodities of primary importance were derived.... It supplied food for immediate and later use, clothing, bedding, shelter, fuel, tools, weapons (in part), household utilities, means for personal or ritualistic adornment, and even the outer "ecclesiastical" symbols of worship.' Several of the numerous appendices also are concerned with Indian customs, beliefs and vocabularies in so far as they related to the bison.

To the question of the total number of the bison population existing at different periods, and their relative density in different areas, Dr Roe devotes six chapters, containing masses of statistics (derived from the descriptions and calculations made by travellers and naturalists, and from the figures relating to the trade in bison hides, meat and bones), 'so as to enable the reader to make some approximate estimate for himself of the once vast numbers'. While of opinion that former suggestions of fifty to sixty millions as the buffalo population in early days are by no means an over-estimate, he concludes by saying that 'no attempt at precise computation, even after the utmost critical caution has been exercised, can be regarded as definitive'.

With reference to the bison in Canada, the author remarks that Hornaday's monograph is devoted primarily to the history of the species in the United States, the Canadian allusions being little more than are required by geographical continuity and for corroboration. Dr Roe discusses the subject in detail in a chapter entitled 'The Historical Habitat of Plains and Wood Buffalo in Canada'.

The only illustration of any kind is the frontispiece showing a bull bison (a fact, incidentally, which makes the price of the book seem high). One would have been glad of something in the nature of maps or diagrams to summarize various aspects of the data so painstakingly accumulated by the author; a map for example on the lines of that in the possession of the United States National Museum, which shows at a glance the original area of North America inhabited by the bison and the gradual shrinking of its range during the nineteenth century; or one like that in Marion Newbigin's *Plant and Animal Geography*, showing the range of the bison in relation to the main types of plant communities. Dr Roe is of course well aware of the existence of maps of this kind—he refers to them in several places—and one or more, embodying such modifications as his researches require, would have been very helpful.

The bibliography of about a thousand titles indicates how thoroughly the author has consulted the available sources; it is in no captious spirit that one suggests that Glover M. Allen's *Extinct and Vanishing Mammals of the Western Hemisphere* (1942) would have been a desirable addition to it.

COLIN MATHESON

THE HABITS OF A RAT

:an M. Linsdale and Lloyd P. Tevis, Jr. (1951). *The Dusky-Footed Wood Rat. A Record of Observations made on the Hastings Natural History Reservation.* Pp. x + 664; 384 text-figures. Berkeley and Los Angeles: University of California Press; London: Cambridge University Press. Price 56*s.* 6*d.*

he most remarkable features of this work are the detail and precision of the field observations, ıe wide range of subject-matter and the extensive documentation. For example, out of 152 ood-rat houses, 52 are described in detail in a chapter of 65 pages crammed with information ıch as this: 'The roof was made of about 180 twigs and branches, from 2 inches to more than 2 inches long; 55 pieces of bark, 2 to 6 inches long; 10 flat pieces of cow dung; 2 rocks, 1 of hich was volcanic; 1 fecal pellet of deer; a clump of matted roots; and nearly 2 quarts of aves. One section of the house wall was a pile of lava rocks ranging from $1\frac{1}{2}$ to $2\frac{1}{2}$ inches ıick.' Clearly there is nothing which has escaped notice, perhaps not even the breed of cow. .t the other end of the scale of treatment the following item, reprinted in its entirety from . 192, makes the most fascinating news story of the decade:

'Pacific Tree-Toad, *Hyla regilla* Baird and Girard
. tree-toad was present in a wood rat house examined on April 10, 1946.'

There are no doubts, then, about the thoroughness of the observations, and those who like acts to speak for themselves may look forward to an interesting recital.

There is a school of thought, however, which believes that facts cannot speak for themselves; hat the essence of knowledge is generalization; that the growth of science is organic, not ccretionary; and that the principal intellectual instrument in research is the hypothesis. Those /ho hold opinions of this sort may find it more difficult to appreciate the present book. Several assages explain how the authors feel about the propositions given above. 'We are not sure', ney say on p. 80, 'that any summary can take the place of the detailed histories and descriptions nat are given.' This is indeed an awkward truth; but a number of thinkers, beginning with the ncient Greeks, have found it more helpful to concentrate on the ways in which observations re alike. We do not all have Newton's audacity to put an apple and a planet into a single lass; nevertheless, the present authors have chosen a most inelegant way of presenting their ata: those, for example on the manner in which wood rat houses are built (described elsewhere s stereotyped).

People who regret the intrusion of statistics into field zoology will perhaps welcome the hapter on population. However, in order to abstract any principles of general validity one nust be possessed of a fair amount of free time and the type of mind that can cope with 0 pages of text and captions, 210 text-figures and photographs and 47 tables (containing, for xample, first and last dates of capture of 288 individuals). The loving care with which these acts are assembled is, I think, explained by two passages: 'every record of an observed elationship of any animal to the wood rat or its habitation is worth preservation'; and especially we want to avoid mistaken interpretation'. The first attitude, though it explains the nysterious passage about the tree-toad, is highly questionable, since it suggests that unselective uriosity is the hallmark of good research. With the aim of the second dictum none can quarrel, ıut it should not have been allowed to lie like a dead hand on discovery or to have been carried o quite the lengths shown in the following: 'Any social ranking or order...lasts only until here is a death or a change in the physical environment or in the health, age or sexual condition f any one rat or all the rats concerned.'

Conclusions occupy less than 0·1% of the total book and, apart from the sort of thing just uoted, are essentially a summary. There is one important point, namely that the population emains fairly stationary, and numerous others such as the comment that wood rats do not eat ılants which are obviously harmful or non-nutritious and that their social structure has everal (unspecified) points of resemblance to that of insects.

According to one's viewpoint, then, this book will seem good or bad. Perhaps the only fair way of looking at it is to recognize the significance of the subtitle and to praise the book as ı first-rate description of specific events. In that case we should no more look for stimulating conclusions than we do in that valuable work by Daniel Webster. On the other hand if rather different criteria are applied it can only be regretted that the style of so monumental a work is Babylonian rather than Greek.

DENNIS CHITTY

BOOKS RECEIVED

Natural Communities. By Lee R. Dice. Ann Arbor: University of Michigan Press. 1952. Price $5.50.

Freshwater Fishery Biology. By Karl F. Lagler. Dubuque, Iowa: Wm. C. Brown. 1952. Price $5.75.

The Changing Wild Life of Britain. By H. L. Edlin. London: Batsford. 1952. Price 21*s*.

The Principles of Line Illustration. By L. N. Staniland. London: Burke. 1952. Price 25*s*.

Faune des Nids et des Terriers en Basse Côte d'Ivoire. By C. Delamare Debouteville and R. Paulian. Paris: Lechevalier. 1952. Price 1350 fr.

N.A.A.S. Quarterly Review. Nos. 17 and 18. London: H.M.S.O. Price 1*s*. 6*d*. per number.

ABSTRACTS

This series of abstracts forms a successor to the 'Notices of publications on the animal ecology of the British Isles' which appeared in the *Journal of Animal Ecology* up to Vol. 20 (1951). Like its predecessor it aims at covering the significant publications in British Journals and Reports dealing with the ecology of the British fauna. Papers published in 1951 will be abstracted, together with those which have appeared more recently, in the next few numbers of the *Journal*. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are papers in *Bird Notes* and *British Birds* which would fall in '4. Food and Food Habits', nor papers in these two journals or in *The Entomologist*, *The Entomologist's Record*, or *The Entomologist's Monthly Magazine* which would be classified in '5. Migration, Dispersal and Introductions'. A special effort is being organized by Mr R. S. R. Fitter with the help of the societies themselves to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations can greatly aid this work by regularly sending copies of their publications to **R. S. R. Fitter, Esq., Greyhounds, Burford, Oxford.**

The abstracts are edited by Prof. L. A. Harvey with the assistance in selection and abstracting of D. H. Chitty, G. I. Crawford, A. E. Ellis, R. S. R. Fitter, Miss U. Grigg, N. A. Holme, A. Macfadyen, C. Matheson, Miss E. Nelmes, and Miss G. Watt. References are checked by B. M. Hobby. Readers and authors can materially assist by pointing out errors and omissions and by sending reprints or offers of help in making abstracts to **Prof. L. A. Harvey, University College, Exeter.**

Separate copies of the abstracts printed on one side of the paper can be obtained from **The Cambridge University Press, 200 Euston Road, London, N.W. 1,** or through any bookseller; price 5*s.* 6*d.* per annum, post free (issued in May and November). Back numbers of the 'Notices of publications ...' from Vol. 3 (1934) to Vol. 20 (1951) may also be had at 2*s.* for each annual set of two parts.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and Brackish

Anon. (1951). Pollution of the Humber. *Min. Agric. & Fish. Investig.* (1) **5** (4), 1–20.

Chemical analysis of the waters of the Humber indicates serious pollution above Hull, mainly derived from the Ouse and Trent. Local effluents into the Humber itself do not appear to present serious problems.

Barnes, H. & Bagenal, T. B. (1951). Observations on *Nephrops norvegicus* (L.) and on an epizoic population of *Balanus crenatus* Brug. *J. Mar. Biol. Ass. U.K.* **30,** 369–380.

Data on the size-frequency, growth and breeding of *Nephrops*. Populations of the epizoic barnacle, *Balanus crenatus*, have been analysed, and growth rate and settling periods determined. The distribution of the barnacle on different parts of the host is described.

Barnes, H. & Bagenal, T. B. (1952). The habits and habitat of *Aporrhais pes-pelicani* (L.). *Proc. Malac. Soc. Lond.* **29,** 101–105.

This species appears to live more on the surface of the sea-floor, and spend less time buried in the mud, than had been supposed.

Barnes, H. & Powell, H. T. (1950). Some observations on the effect of fibrous glass surfaces upon the settlement of certain sedentary marine organisms. *J. Mar. Biol. Ass. U.K.* **29,** 299–302.

A description is given of a glass cloth surface which prevents the settlement of larvae of *Balanus crenatus* and *Pomatoceros triqueter*, whilst not affecting that of *Tubularia larynx*. A number of possible reasons for this are examined.

Chang, H. W. (1951). Age and growth of *Callionymus lyra* L. *J. Mar. Biol. Ass. U.K.* **30,** 281–296.

An account of the growth and breeding of this species. The radial bone is used for age determination and results accord with otolith readings.

Cole, H. A. (1952). The American slipper limpet (*Crepidula fornicata* L.) on Cornish oyster beds. *Min. Agric. & Fish. Fish. Investig.* (2) **17** (7), 1–13.

Reviews the occurrence of *Crepidula* in Falmouth Harbour and Helford River since 1946. Only single occurrences from Falmouth, but several chains found in Helford River. Examines possible means of immigration and concludes that ship transportation only is possible. Suggests control measures.

Cushing, D. H. (1951). The vertical migration of planktonic Crustacea. *Biol. Rev.* **26,** 158–192.

Earlier and new records are shown to conform to a sequence of four stages: (*a*) evening ascent from day depth, (*b*) midnight sinking, (*c*) dawn rise and (*d*) descent to day depth. These stages are shown to be part of a single process of adjustment to an optimum light intensity, (*b*) being a passive phase in the absence of light. Other theories are considered critically and evidence quoted to show that migration is mediated by light penetration and both oriented by its direction (phototaxis) and regulated by its intensity (photokinesis).

Digby, P. S. B. (1950). The biology of the small planktonic copepods of Plymouth. *J. Mar. Biol. Ass. U.K.* **29,** 393–438.

An account of the abundance, growth, and reproduction of nine species.

Forster, G. R. (1951). Notes on *Leander squilla* L. *J. Mar. Biol. Ass. U.K.* **30,** 361–367.

A brief account of growth, food and the habitat of this species, as contrasted with *Leander serratus*.

Forster, G. R. (1951). The biology of the common prawn, *Leander serratus* Pennant. *J. Mar. Biol. Ass. U.K.* **30,** 333–360.

An account of the growth, breeding and migrations of this species from observations extending through one year at Plymouth.

Galliford, A. L. & Williams, E. G. (1948). Microscopic organisms of some brackish pools at Leasowe, Wirral, Cheshire. *Northw. Nat.* **23,** 39–62.

Includes lists of Entomostraca, Rotifera (with indications of salinity and seasonal abundance), Gastrotricha, Protozoa and Dinoflagellates found in a survey begun in 1945, with an account of the history of the pools, which are thought to be artificial, and the ecological conditions within them.

Harvey, H. W. (1950). On the production of living matter in the sea off Plymouth. *J. Mar. Biol. Ass. U.K.* **29**, 97–137.

A survey of producers and consumers of food in the sea. Estimates are given of the quantity of the standing crop and the daily production of plants and animals below a square metre, in the English Channel. A preliminary 'balance sheet' has been drawn up to indicate the magnitude of the daily increase in weight and loss through respiration, and the annual mortality. There is a brief discussion of changes in the fertility of the sea.

Harvey, L. A. (1952). The slate shores of Lundy. *Ann. Rep. Lundy Field Soc.* **5** (1951), 25–29.

A preliminary account of the invertebrate fauna of the slate shores of a Bristol Channel island.

Holme, N. A. (1950). The bottom fauna of Great West Bay. *J. Mar. Biol. Ass. U.K.* **29**, 163–183.

Account of species taken in the bottom-sampler, mostly on a line running south from Exmouth to position east of Start Point. A large bed of *Turritella communis* occurs near Torbay; and a dense bed of *Spisula solida* in Start Bay, previously found by E. Ford in 1923, is still in existence.

Knight-Jones, E. W. (1951). Gregariousness and some other aspects of the setting behaviour of *Spirorbis*. *J. Mar. Biol. Ass. U.K.* **30**, 201–222.

Many more larvae settled on pieces of *Fucus* which bore previously settled *Spirorbis* than on bare controls. Larvae settled more readily on blocks bearing their own species than on blocks bearing another species of *Spirorbis*. The significance of gregarious settlement in marine larvae is briefly discussed.

Knight-Jones, E. W. & Stephenson, J. P. (1950). Gregariousness during settlement in the barnacle *Elminius modestus* Darwin. *J. Mar. Biol. Ass. U.K.* **29**, 281–297.

Settlement of larvae is heavier on glass plates bearing recently settled barnacles than on similar bare areas. Similarly, settlement is heavier on plates placed on the shore where adults are abundant than on plates in a muddy area where adults are absent. It is suggested that the sensory basis for gregariousness can act at a distance, and that it may possibly be olfactory.

Menon, M. D. (1950). Bionomics of the poor-cod (*Gadus minutus* L.) in the Plymouth area. *J. Mar. Biol. Ass. U.K.* **29**, 185–239.

Detailed account of the food, growth rate and spawning period of this species. Age and growth rate have been computed from the size of growth rings on the supra-occipital crest: these show a good correlation with age as determined by scales, otoliths and size-analysis.

Mistakidis, M. N. (1951). Quantitative studies of the bottom fauna of Essex oyster grounds. *Min. Agric. & Fish. Fish. Investig.* (2) **17** (6), 1–47.

Records surveys with Petersen grab of two semi-derelict oyster grounds in the rivers Crouch and Roach, both dominated by *Crepidula* and carrying few oysters except on cleared and re-stocked areas. *Irosalpinx cinerea* is confined largely to firm shelly ground and absent from pure mud. *Cardium exiguum* is common to both grounds, *Abra alba* is scarce and *Macoma balthica* common in the Roach, the reverse holding in the Crouch which has less mud and a lower organic content. The reduced silt in the Roach is thought to account for the greater abundance and variety of ascidians and sponges there. Quantitative fauna lists are given and analysed in relation to oyster culture.

Myefinch, K. A. (1950). Studies on marine fouling organisms. *J. Iron and Steel Inst.* **165**, 214–220.

A summary of the work done on the biological aspects of the fouling problem, mainly at Millport, during the period 1944–48.

Quick, H. E. (1950). Observations on *Limapontia*. *Proc. Malac. Soc. Lond.* **28**, 134–138.

Notes on the anatomy, habits and habitats of two species of Saccoglossan Gastropods, *Limapontia depressa* and *L. capitata*.

Sergeant, D. E. (1951). The status of the common seal (*Phoca vitulina* L.) on the East Anglian coast. *J. Mar. Biol. Ass. U.K.* **29**, 707–717.

A study of the food, population, and ecology of this species. While seals on the open coast feed largely on fish, those in the Wash have become adapted to feeding on shellfish in the absence of large populations of fish.

Spooner, G. M. (1951). On *Gammarus zaddachi oceanicus* Segerstråle. *J. Mar. Biol. Ass. U.K.* **30**, 129–147.

An account of the distribution of this subspecies in Britain and the North Atlantic coasts. The ecological relations between *G. z. oceanicus*, on the one hand, and *G. z. salinus* and *G. locusta*, on the other, are discussed.

Steven, G. A. (1952). Contributions to the biology of the mackerel, *Scomber scombrus* L. III. Age and growth. *J. Mar. Biol. Ass. U.K.* **30**, 549–568.

Direct age-readings from scales and otoliths have been made, for the first time in this species, for fish up to 6 years of age. There appears to be a change in the growth characteristics at a length of about 29 cm., coinciding with the first ripening of the genital products.

Vevers, H. G. (1951). Photography of the sea floor. *J. Mar. Biol. Ass. U.K.* **30**, 101–111.

An underwater photographic apparatus is described for taking a series of pictures of the sea floor, each of 1 m.^{2}, at depths of at least 80 m. Dense aggregations of *Ophiothrix fragilis* have been photographed in one area.

Wilson, D. P. (1951). A biological difference between natural sea waters. *J. Mar. Biol. Ass. U.K.* **30**, 1–20.

Eggs and larvae of *Echinus esculentus*, *Ophelia bicornis* and *Sabellaria alveolata* developed abnormally, or were in poor health, in sea water collected from the English Channel near the Eddystone, but in water collected in the Celtic Sea (west-north-west of Land's End), development was generally normal and healthy.

Experiments indicated that Channel water lacked some unknown constituent, essential for healthy development, which was present in the Celtic Sea water. The results accord with some hydrographical and biological changes in the area which have taken place within recent years.

Yonge, C. M. (1951). Observations on *Sphenia binghami* Turton. *J. Mar. Biol. Ass. U.K.* **30**, 387–392.

The mode of life of this lamellibranch, adapted for life attached by a byssus in crevices, is described.

(*b*) Fresh Water

Corbet, P. S. (1950). Some observations on *Ceriagrion tenellum* (Villers) (Odonata). *Entomologist*, **83**, 27.

Adults were abundant along a peat runnel during drought in July 1949, whereas those of *Pyrrhosoma nymphula* were relatively scarce. No nymphs of *C. tenellum* were found, though those of *Pyrrhosoma nymphula* were plentiful. It is suggested that, under certain conditions, *C. tenellum* can metamorphose after one year, which benefits the species in removing the nymphs from an unfavourable environment. In *P. nymphula*, either a two-year larval stage is obligatory or drought in summer is too late to influence its development.

Gray, E. (1952). The ecology of the ciliate fauna of Hobson's Brook, a Cambridgeshire chalk stream. *J. Gen. Microbiol.* **6**, 108–122.

The ciliate fauna is largely that of the adjacent banks and is highest after rain and when banks crumble in dry weather. High ciliate populations are associated with green and blue-green filamentous algae. They are not correlated with bacterial density except that the latter, especially Gram-positive rods, are highest where diatom feeding ciliates occur. Gram-negative rods abound with bacterial-eating ciliates. Cycles of ciliate abundance are reported.

Savage, R. M. (1952). Ecological, physiological and anatomical observations on some species of anuran tadpoles. *Proc. Zool. Soc. Lond.* **122**, 467–514.

The biology of a number of separate populations was followed in three seasons and in feeding and growth rates marked differences, even between populations in the same pond, occurred. Since the gut is usually filled with detritus when food is not to be found, the gut content is little indication of true food. Starvation is common in dense populations. Material passes through the gut very rapidly and only mechanically ruptured cells are digested. Entomostraca are commonly eaten by large tadpoles, but algae are the commonest food. The feeding mechanisms of *Rana* and *Bufo* are described and compared; a microphagous mechanism employing strings of mucus and a centrifugally precipitating mechanism for larger particles are described.

Stratton, L. W. (1951). The Mollusca of Elstree Reservoir. *J. Conchol.* **23**, 147–149.

Since 1919 the number of species in the reservoir has increased from about 8 to 21, and the range of a number of species has extended.

Talling, J. F. (1951). The element of chance in pond populations. *Naturalist*, 157–170.

Despite the conclusions of certain observers that there is a considerable element of chance in pond populations, the supporting evidence is often ambiguous. There are certain indications that the obvious physical barriers between populations are usually overcome by the efficacy of dispersal.

Whitaker, M. B. (1951). On the homologies of the oesophageal glands of *Theodoxus fluviatilis* (L.). *Proc. Malac. Soc. Lond.* **29** (1), 21–34.

T. fluviatilis is found in rivers of chalk and limestone districts, and is numerous where clear water rushes over stones: it feeds on minute algae collected by the radula.

Whitehead, H. (1952). The natural history of some Yorkshire rivers. *Naturalist*, 1–6.

Deals mainly with the relationship of the fauna to the nature of the stream bed. Most of the observations are based on material taken from rivers rising in the Pennines, but a comparison is made with a river—Driffield Beck—which rises in the Wolds.

(*c*) Land

Allen, A. A. (1951). The Coleoptera of a suburban garden. 1. Adephaga. *Ent. Rec.* **63**, 61–65. (2. Palpicornia, Lamellicornia, Serricornia. *Ibid.* **63**, 187–190.) (3. Heteromera, Longicornia, Phytophaga. *Ibid.* **63**, 256–259.) ((1952). 4. Rhynchophora. *Ibid.* **64**, 61–63, 92–93.)

A list of 168 beetles found in a garden, some 20 years old, in a fairly well built-up area in Greater London, with notes on habitats, food plants, abundance, seasonal appearance and dates. The garden, which is almost entirely cultivated and without any large trees, is half an acre in extent, but one less than half this size would probably contain as many species.

Blackie, J. E. H. (1948). The birds of a Manchester housing estate. *Northw. Nat.* **23**, 83–87.

An annotated list, giving abundance and status and including the results of a census of rookeries and nests. Lists are also given of birds formerly present in the area and of birds absent from it, but present in an adjacent one.

Brian, M. V. & Brian, A. D. (1951). Insolation and ant population in the West of Scotland, *Trans. R. Ent. Soc. Lond.* **102**, 303–330.

Colonies of *Myrmica rubra* in open canopy woodland, by contrast with those in exposed short herbage, are smaller, retarded in brood development, sterile and with smaller workers. Experimental investigation of the deficiencies, except sterility, show that the lower temperature of the shaded habitat accounts for them. The smallness of workers is due to food-deficiency induced partly by lowered activity, partly by more distant separation from sources of sugar. Analysis of subseres from felled woodland and burned heather show population maxima at the beginning, with decline as vegetation encroaches.

Brown, J. J., Kersley, L. W. & MacDonald, R. (1951). Notes on the flora and fauna of the Maidens. *Irish Nat. J.* **10**, 208–211.

A general account of all species found on two brief visits to Mere islands off Co. Antrim. As the total time spent ashore was only 4 hr., and as the tide was full on both occasions the sample of species found is necessarily meagre. The paper, however, provides a useful introduction to the type of fauna found on these islands.

Carpenter, G. D. H. (1950). Some insects (excluding Lepidoptera) from the Shetland Isles. *Ent. Mon. Mag.* **86**, 268–269.

Cloudsley-Thompson, J. L. (1951). On the responses to environmental stimuli, and the sensory physiology of millipedes (Diplopoda). *Proc. Zool. Soc. Lond.* **121**, 253–277.

Reactions to environmental stimuli are described, temperature has a threefold effect on locomotion; sudden changes stimulate movement, a preferendum is sought and activity varies with temperature level. Reactions to humidity, chemicals and vibrations are discussed. An attraction to sugars is probably ecologically, and in pest species economically, important.

Cloudsley-Thompson, J. L. (1951). Studies in diurnal rhythms: 1. Rhythmic behaviour in millipedes. *J. Exp. Biol.* **28**, 165–172.

With two British species numbers visible at surface of a dish were noted at intervals. Activity rhythm depends on light and disappears in continuous light or dark; is independent of feeding. Rapid cooling in evening stimulated activity. Two tropical species in an aktograph, however, had 'endogenous' rhythms independent of light and temperature; here too sudden temperature changes have a stimulatory effect.

Comfort, A. (1951). Distribution of *Hygromia cinctella* (Draparnaud) at Paignton. *J. Conchol.* **23**, 136.

Habitats of a species of snail recently discovered in South Devon.

Conder, P. J. (1951). The factors affecting the distribution of wheatears on Skokholm. *Rep. Skokholm Bird Observatory*, 1950, 15–19.

The normal habitat of *Oenanthe oenanthe* is open country with no overhead cover. This prevails all over the Pembrokeshire island of Skokholm, where the bracken does not provide overhead cover until most pairs have started breeding. The rabbit is the most important single factor, both by grazing the vegetation to a height which suits the wheatear's gait, and by providing many of the nesting-holes.

Cottam, R. (1948). On new methods of controlling ground wasps. *Northw. Nat.* **23**, 127–129.

Fifty-six queens were trapped during May-June 1948 in a decoy, queenless nest of *Vespula vulgaris*, which was ultimately taken over by a queen of *V. austriaca*. Fifty-eight queens of *V. vulgaris*, thirty of *V. rufa*, thirty-three of *V. germanica* and one of *V. austriaca* were netted while foraging on vegetation in a hedgebank and weed-covered ground over a period of 30 days. Workers from five nests of *V. vulgaris* were small, indicating that they had lost their queens and been deprived of food as larvae; all had acquired new queens. A nest of *V. sylvestris* was found 1 ft. away from one of *V. vulgaris*, with another of *V. vulgaris* 3 yards away.

Cramp, S. & Teagle, W. G. (1952). A bird census of St James's Park and the Green Park, 1949–50. *Lond. Bird Rep.* **15**, 48–52.

Of totals of twenty-eight and twenty-nine birds noted, respectively, on monthly visits to St James's Park (52 acres) during November 1949–March 1950 and on three visits to Kensington Gardens (274 acres) during 1948–49, twenty-two were common to both parks. Duck were more and gulls less numerous in St James's Park. The dominant land birds were house-sparrow, blackbird, wood-pigeon, starling and blue tit, and their relative abundance in the two parks was similar. The density of land birds in the four habitats common to both parks was 265·3 per 10 acres in Kensington Gardens and 129·7 in St James's Park, and that of water birds was 478·1 and 882·2, respectively, In the Green Park (53 acres), where there is no water, only fifteen land birds were noted. It contains only two of the nine habitats recognized in Kensington Gardens, but owing to the numbers of house-sparrows, their density is more than six times as great as in similar habitats in Kensington Gardens, which has nineteen land birds. The dominant land birds in the Green Park were house-sparrow, blackbird, starling, wood-pigeon and chaffinch, and the relative abundance of the first four and blue tits was similar to that in the other two parks.

Edney, E. B. (1951). The body temperature of woodlice. *J. Exp. Biol.* **28**, 271–280.

Temperature only differs from surroundings in dry air, when a lowering of up to 6·8° at 37° C., depending on species, is found. The capacity to evaporate water rapidly may be of survival value over short periods.

Ellis, A. E. (ed.) (1951). Census of the distribution of British non-marine Mollusca. *J. Conchol.* **23**, 171–244.

British and foreign distribution, geological distribution, brief notes on habitat, tables of vice-comital distribution, maps. The 7th edition of the Census of land and freshwater Mollusca begun by the Conchological Society in 1876.

Evans, W. (1951). An ecological survey of hill sheep farming in Breconshire. *Agriculture*, **58**, 5–13.

Lists and describes the breeds of sheep favoured in different areas and discusses their relations to altitude, rainfall, rock formation and pasturage.

Fidler, J. H. (1948). The biology of some Yorkshire Aphides, II. *Northw. Nat.* **23**, 103–112,

An annotated list of species found in 1947 and 1948, with stages, food plants, dates, localities and other miscellaneous observations, and a shorter list of alates taken in adhesive traps with dates and localities.

Frazer, J. F. D. (1951). Notes on a colony of *Colias crocea* Fourcroy. *Entomologist*, **84**, 25–29.

Contains some observations on behaviour, means of dispersal and factors affecting development.

Haggett, G. (1950). The life history and habits of *Zeuzera pyrina* Linn. (*aesculi* Linn.) in Britain. *Entomologist*, **83**, 73–81.

A detailed account of observations in West Sussex on the bionomics, of which little is known. The natural habitat appears to be young trees and saplings in wooded country, but any other providing suitable growth is used. Ash is the principal food plant and privet of suitable thickness is also attacked, but incidence in other plants is low; in built-up areas, the larvae are recorded most frequently from lilac. Stems and branches up to 4 in. in diameter are attacked and those from 1½ to 2½ in. are preferred. The larvae and adults are attacked by birds; no parasites were found.

Hacker, H. P. & Pearson, H. S. (1951). Distribution of the long-tailed field mouse, *Apodemus sylvaticus*, on South Haven Peninsula, Dorset, in 1937, with some observations on its wandering and homing powers. *J. Linn. Soc. Lond.* **42**, 1–17.

Mice were trapped in over fifty habitats but relative preferences were not established owing to the methods used. A general preference was found for woodland over heathland. Re-trapping of marked mice showed a normal range over more than 200 yards from the nest with possibilities of homing up to 1000 yards, traversing normally uninhabited country, such as bogs and swamps, *en route*.

Harrison, J. W. Heslop (1950). A wasp, *Vespula rufa* L. (Hym., Vespidae) new to the Outer Hebrides. *Ent. Mon. Mag.* **86**, 298.

Harrison, J. W. Heslop (1950). Observations on the ranges, habitats and variation of the Rhopalocera of the Outer Hebrides. *Ent. Mon. Mag.* **86**, 65–70.

Harrison, J. W. Heslop (1950). Lepidoptera in the Outer Hebrides in 1950. *Entomologist*, **83**, 241–245.

Includes some extensions of range and a few species new to these islands.

Harrison, J. W. Heslop (1950). *Perizoma flavofasciata* and *Hadena bicruris* added to the fauna of the Isle of Eigg. *Entomologist* **83**, 42.

Harrison, J. W. Heslop (1950). *Scoliopteryx libatrix*, a moth new to the Hebrides, in the Isle of Rhum. *Entomologist* **83**, 30.

Henstock, H. (1950). Experiments with a light trap at Caerwys, North Wales, during the years 1947, 1948 and 1949. *Entomologist* **83**, 175–188.

The light trap was operated continuously from March until the end of October. A fall in temperature is associated with a fall of total catch and a rise in temperature by a rise in total catch. The minimum night temperature falls at or near the full moon and this drop is closely followed first by a rise and then by another fall. Noctuids predominate over Geometrids in March, April, June, July and September and Geometrids over Noctuids in May, August and October. In each of eight species for which analyses were made the number caught per year showed an inverse relationship to the number of moonlight nights that occurred during the period over which they were trapped.

Hewson, R. (1948). Some observations on the Orkney vole, *Microtus o. orcadensis* (Millais). *Northw. Nat.* **23**, 7–10.

Descriptions and plans of underground tunnels, nesting chambers and burrows from various localities.

Hincks, W. D. (1951). The entomology of Spurn Peninsula. *Naturalist*, **1951**, 75–86, 139–146, 183–190.

Concludes the general entomology of the area, including that of Kilnsea Warren, the salt-marsh and the Humber foreshore. The orders 'Orthopteroid' and 'Neuropteroid' and the Hemiptera and Lepidoptera are treated in detail.

Howe, R. W. (1950). The development of *Rhizopertha dominica* (F.) (Col., Bostrichidae) under constant conditions. *Ent. Mon. Mag.* **86**, 1–5.

In cultures in wholemeal flour at 70% relative humidity, the number of larval instars varied, being sometimes reduced to 3 at 28° C. and sometimes increased to 5–6 at 25° C. Few larvae with extra instars survived. Larval mortality was 20% at 25° C. and 9% at 28° C. At 25° C., females laid totals of 52–561 eggs in periods of 11–43 days. Development was faster in whole grain than in flour ground from it.

Laurence, B. R. (1950). Syrphidae (Diptera) in Bedfordshire. *Ent. Mon. Mag.* **86**, 351–353.

Thirty-five species collected during 1944–49 from woodland and permanent pasture with streams and hedges on Gault clay are listed according to whether caught in one or several years, and whether in woodland, outside woodland or in both habitats. Topographical and ecological descriptions of the area are given.

London Natural History Society (1952). City bombed sites survey. *Lond. Nat.* **31**, 83–91.

C. J. F. Bensley lists the molluscs found on two visits, which, in addition to two colonies of *Helix aspersa*, comprised only four species, all confined to old gardens. D. F. Owen lists the 44 Lepidoptera observed in the area and discusses the factors affecting their incidence. P. W. E. Currie discusses the twelve sawflies known to be present in a similar manner and gives dates, localities and food plants.

London Natural History Society (1951). The Survey of Bookham Common—Ninth year. *Lond. Nat.* **30**, 41–72.

An introductory progress report of work in 1950 includes notes by C. J. F. Bensley on the recolonization of recently drained ponds, streams and ditches by freshwater molluscs and by M. Niblett on Trypetids, Cynipids and Cecidomyiids observed during the year, including some new records for the area. A. L. Panchen gives notes on the distribution and status of the reptiles and Amphibia. A. E. le Gros gives an initial list of 100 spiders, excluding Linyphiids, recorded from the Common with their relative frequencies, distribution and habitats, the relative abundance of each family in different habitats, and preliminary observations on the extent of parasitism. G. Beven gives a detailed account of a survey made during 1946–50 of the bird population of an oakwood (40 acres), which contained the territories of 23–24 robins, at least 16 wrens, 19 wood warblers, 2 chiff-chaffs, 6 blackbirds and 9 chaffinches; 32 species were recorded in the wood, and 28 were present in the breeding season. The fluctuations in the total bird population throughout the year are discussed, with special reference to the movements of tits and chaffinches. Robin territories were most numerous (18 per 10 acres) in hawthorn secondary growth exceeding 50 bushes per 800 sq.yd.; they decreased progressively as the hawthorn thinned, and reached a minimum of 1·4 per 10 acres where there were only 5–10 bushes per 800 sq.yd.

London Natural History Society (1952). The survey of Bookham Common—Tenth year. *Lond. Nat.* **31**, 33–62.

Following an introductory progress report of work in 1951, C. J. F. Bensley describes the recolonization of a pond by freshwater molluscs following cleaning and repairs; the relative proportions of the common Gastropods present before and after the repairs showed considerable differences, and the

umber and species in ditches and streams were both greatly reduced after clearing. A. M. Easton sts about 100 Geodephaga recorded during 14 years, with months, localities, habitats and abundance. I. Niblett gives a supplementary list of Diptera, based on larvae reared from plants. D. Leston lists ne Heteroptera, giving dates and, for some, habitats, and discusses the Corixid fauna and population f a pond with reference to status and habitat requirements; he appends a list of aquatic Coleoptera,

McMillan, Mrs N. F. & Stelfox, A. W. (1952). Survey of Inistrahull: Pt. 6. (Report on Mollusca collected by Messrs Ranald MacDonald, B.Sc., and D. J. Sullivan). *Irish Nat. J.* **10**, 232–235.

Notes on the land and marine Mollusca found on an island off north-west Ireland. The list of marine orms is not regarded as complete.

Mellish, W. D. (1952). The census of Great Crested Grebes, 1950 and summary of results, 1946 to 1950. *Lond. Bird Rep.* **15**, 46–48.

The total number of *Podiceps cristatus* in the London area showed a further rise, estimated at 34%, n 1950, the most notable increases being in Bucks. and on waters other than gravel-pits in Surrey, vhere they respectively reached and exceeded 100%. The birds were again more numerous on lakes ind reservoirs than at gravel-pits, and 149 nesting pairs were reported. Numbers of adult birds have ncreased by 57% since 1946.

Miles, M. (1951). The spinach stem fly. *Agriculture* **58**, 332–334.

Notes the occurrence, life history and injury caused by *Hylemyia echinata* on spinach at Wye and suggests that it may be widely distributed in Britain.

Miles, M. (1951). Some aspects of cabbage root fly attack in the field. *Agriculture*, **58**, 234–237.

Lists species attacking *Brassica* crops and discusses effects of soil temperature and moisture in determining time of emergence and egg-laying. The flies live for several weeks and 3rd-generation egg-laying females may occur into October.

Murgatroyd, W. E. (1950). The spider population of disused bee-hives. *Ent. Mon. Mag.* **86**, 251.

Five disused bee-hives, with a few living and dead bees, each contained 30–40 female and immature *Stearodea bipunctata*, 10–15 *Harpactia hombergi* including both sexes, 5–6 female *Tegenaria domestica*, 2–4 females of *T. atrica*, and 1 or 2 female or immature *Ciniflo similis* in April 1950.

Parrinder, E. R. (1952). Interim report on the starling enquiry. *Lond. Bird Rep.* **15**, 58–59.

Results over 3 years show that the number of starlings roosting in Central London each night varies from 10,000 to 100,000, with maximum numbers in June–July, when trees are used. Most birds return to roosts on buildings in October. Few continental birds use the London roosts. Of 125 birds ringed in Trafalgar Square, and subsequently recovered, only two were found abroad; most of the rest were within 20 miles of the roost and in the area defined by tracing flight lines. Details of some recoveries of birds ringed in Trafalgar Square and in the suburbs are included.

Parry, D. A. (1951). Factors determining the temperature of terrestrial arthropods in sunlight. *J. Exp. Biol.* **28**, 445–462.

Reports thermocouple measurements in metal models near the ground; the temperature depends on distance above ground and its temperature. Results agree with similar measurements on a locust. A theoretical discussion of the influence of orientation, size, wind speed, colour and shape on heat uptake; all these are important and leave much scope for behavioural responses. Metabolism and evaporation are unimportant. Steep temperature gradients near the ground make measurements difficult and also stress importance of behaviour.

Peacock, A. D. (1950). Studies in Pharaoh's ant, *Monomorium pharaonis* (L.). 2. Methods of recording observations on artificial colonies. *Ent. Mon. Mag.* **86**, 129–135.

Savage, C. D. W. (1950). Some notes on the Mandarin Duck (*Aix galericulata*) in this area. *Middle-Thames Nat.* **3**, 13–15.

A brief account of the apparent natural establishment and spread of a colony in Windsor Great Park, with notes on display, nesting sites, feeding habits and natural enemies.

Shorten, M. (1951). Some aspects of the biology of the grey squirrel (*Sciurus carolinensis*). *Proc. Zool. Soc. Lond.* **121**, 427–459.

The British population is described and contrasted with the American with special reference to taxonomy, mutants and their distribution, sex ratios, breeding seasons and rates, litter-size, nesting behaviour and site preferences. Experiments with captive animals on breeding and rearing are described and full records of growth and development given; a too lavish food supply inhibited breeding. An age/body-weight curve calculated from captives is correlated with data from wild animals. Census methods are considered and a warning against uncritical use of drey counts given.

Stephens, M. N. (1952). Seasonal observations on the wild rabbit (*Oryctolagus cuniculis* L.) in West Wales. *Proc. Zool. Soc. Lond.* **122**, 417–434.

Statistics are given on weight, reproduction, sex ratios, refection, diseases and parasites in over 7000 rabbits. The main breeding season was January to June. Pre-natal sex ratio was 100 male to 106 female and there was a significant tendency for females to occur in the left, males in the right uterine horn. Sex ratios obtained are compared to Brambell's figures. Infestations with tape-worms were very high, cysts were rare in young rabbits, and therefore in the population as a whole in spring. *Eimeria stiedae* was commonest in 6–10-week rabbits, *Fasciola hepatica* was confined to wet, non-maritime districts.

Temperley, G. W. (1951). A history of the birds of Durham. *Trans. Nat. Hist. Soc. Northumb., Durham Newcastle upon Tyne* (N.S.), **9**, 296.

The first complete modern list of the birds of a county which, in the past, has been largely overshadowed by its neighbours. Contains descriptions of the varying habitats with their typical birds and traces the effect of change of environment, in particular the industrialization of the eastern part of the area, on the bird life. Includes accounts of bird movements on the coast, the development of protection, museums and collections and former Durham ornithologists. A brief description is given of the present and past status of each species recorded.

Venables, L. S. V. & Venables, U. M. (1950). The whooper swans of Loch Spiggie, Shetland. *Scot. Nat.* **62**, 142–152.

Food, population statistics, mobility, family size and percentage of cygnets in a herd of up to 88 *Cygnus cygnus* during three winters.

Verdcourt, B. (1951). Land snails of a residential area in N.W. Hertfordshire. *J. Conchol.* **23**, 155–157.

Thirty-two species recorded from a garden and orchard in a built-up area, with notes on habitat, etc

Williamson, K. (1951). The moorland birds of Unst, Shetland. *Scot. Nat.* **63**, 37–44.

A consideration of the ecological factors affecting the breeding status of the birds of the northernmost of the British Isles.

Woodroffe, G. E. & Southgate, B. J. (1951). Birds' nests as a source of domestic pests. *Proc. Zool. Soc. Lond.* **121**, 55–62.

Useful lists of inhabitants of the nests of five species of house-nesting birds include a number of stored-products and domestic pests; outstanding are clothes moths, house moths, carpet beetles, silverfish and stored-products mites. Ecological information on the environment and feeding habits of the animals is given and three successional stages are recognized, typified by bird ectoparasites, stored-products forms and a humus fauna resp.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Barnes, H. & Bagenal, T. B. (1951). A statistical study of variability in catch obtained by short repeated trawls taken over an inshore ground. *J. Mar. Biol. Ass. U.K.* **29**, 649–660.

Results suggest some degree of aggregation of fish populations.

Bradley, J. D. (1951). *Micropteryx kaltenbachii* Wood 1890 synonymous with *Eriocrania chrysolepidella* Zeller 1851 (Lep. Eriocraniidae). *Entomologist*, **84**, 9–10.

China, W. E. (1950). A check list of the British Hemiptera-Homoptera Auchenorhyncha. *Ent. Mon. Mag.* **86**, 243–251.

Collin, J. E. (1951). The British species of the genus *Palloptera* Fallen (Diptera). *Ent. Rec.* **63** (5), suppl. 6 pp.

A key, with notes on distributions, seasons and habitats.

Crosskey, R. W. (1951). The morphology, taxonomy, and biology of the British Evanioidea (Hymenoptera). *Trans. R. Ent. Soc. Lond.* **102**, 247–301.

Part I deals with morphology, Part II with taxonomy and biology and contains a key to British representatives followed by descriptions of species with notes on adult habits and larval hosts.

Freeman, R. B. (1950). A check list of the British Siphonaptera, with comments on the nomenclature. *Ent. Mon. Mag.* **86**, 14–22.

Holme, N. A. (1950). Population-dispersion in *Tellina tenuis* da Costa. *J. Mar. Biol. Ass. U.K.* **29**, 267–280.

A population of this lamellibranch is shown to be uniformly distributed, indicating a significant degree of 'over-dispersion'. There is a tendency for individuals to spread out so that the distance of each individual from its nearest neighbour is greater than would be expected if the animals were distributed at random. It is suggested that this spacing is correlated with the foraging activities of the inhalent siphon on the surface of the sand.

Johnson, D. S. (1952). The British species of the genus *Daphnia* (Crustacea, Cladocera). *Proc. Zool. Soc. Lond.* **122**, 435–462.

An account of the genus with keys to females and males; the taxonomic value of the latter is stressed. Notes on distribution within and outside Britain.

Kimmins, D. E. (1951). A note on the females of the British species of Beraeidae (Trichoptera). *Entomologist*, **84**, 19–21.

Includes a key for separating both sexes of the British species.

Leslie, P. H., Venables, U. M. & Venables, L. S. V. (1952). The fertility and population structure of the brown rat (*Rattus norvegicus*) in corn-ricks and some other habitats. *Proc. Zool. Soc. Lond.* **122**, 187–238.

An analysis of the demography of rat populations, mainly from corn ricks, covering nearly 4000 animals, including calculations of fertility, life tables, infant mortality, rates of increase and stable age distributions. Methods and significance of these parameters are discussed. The pregnancy or embryo rate per female are recommended as measures of population fertility. A very marked difference in fertility between females inside and those outside the ricks in winter months was observed. The annual peak of fertility was in April. The inherent rate of increase approached 0·1 per head per week.

MacNeill, N. (1951). Separation characters for nymphs of *Lestes dryas* Kirby and *L. sponsa* (Hansemann) (Odonata–Lestidae). *Entomologist*, **84**, 40–42.

The length of the caudal lamellae is useless as a separation character, but their shape and the morphology of the labial masks can be used.

Mann, K. H. (1952). A revision of the British leeches of the family Erpobdellidae, with a description of *Dina lineata* (O. F. Müller, 1774), a leech new to British fauna. *Proc. Zool. Soc. Lond.* **122**, 395–405.

The genital atrium is used to distinguish the leeches. The habitat of *Dina lineata* is described. The relative ecological demands of *Erpobdella testacea* and *E. octoculata* are discussed. The maintenance of two varieties for the latter is deprecated. Records for *Trocheta subviridis*, especially at sewage works, are given. This leech is amphibious and thereby attracts attention.

Muldal, S. (1952). A new species of earthworm of the genus *Allolobophora*. *Proc. Zool. Soc. Lond.* **122**, 463–465.

A. minima sp.nov. was probably previously overlooked on account of its resemblance to immature specimens of other species in the genus.

Quick, H. E. (1952). Rediscovery of *Arion lusitanicus* Mabille in Britain. *Proc. Malac. Soc. Lond.* **29**, 93–101.

Arion lusitanicus had been omitted from the British list because the only British record (from Bantry Bay) was considered dubious. Specimens are now recorded from Durham near the river at North Bailey. Dissection confirms their specific distinctions from *A. ater* (L.), *A. rufus* (L.) and *A. subfuscus* (Drap.).

Rees, C. B. (1950). The identification and classification of lamellibranch larvae. *Hull Bull. Mar. Ecol.* **3** (19), 73–104.

An account of a method of identifying post veliger lamellibranch larvae, employing chiefly the shape of the shell and the structure of the hinge. The method is especially useful for preserved specimens, in which the soft parts may be unrecognizable. Seventy-seven types from the North Sea are described, twenty-eight being assigned firmly to species and tentative suggestions of generic or specific affinities being put forward for many of the others.

Russell, F. S. (1951). A re-examination of *Calanus* collected off Plymouth. *J. Mar. Biol. Ass. U.K.* **30**, 313–314.

A re-examination of some collections of the copepod *Calanus finmarchicus* made off Plymouth has shown that the conclusions reported in certain previous publications by Russell and others can be regarded as referring to the form *helgolandicus*.

Sexton, E. W. & Reid, D. M. (1951). The life-history of the multiform species *Jassa falcata* (Montagu) (Crustacea, Amphipoda) with a review of the bibliography of the species. *J. Linn. Soc. Lond.* **42**, 29–91.

An amply illustrated account of this very common and markedly polymorphic amphipod, with experimental breeding records and descriptions of young forms liable, otherwise, to cause confusion.

Sweeney, R. C. H. (1950). Some new formicaria and other practical aids to the study of ant colonies. *Ent. Mon. Mag.* **86**, 110–116.

Tucker, D. G. (1951). The application of the logarithmic series and the index of diversity to bird population statistics. *Lond. Nat.* **31**, 62–80.

When the logarithmic series and the index of diversity were applied to extensive data on bird populations, it was found that the former fits the observed results reasonably well, though a hyperbolic series might prove superior. Where comparable data for winter and the breeding season were available, the index of diversity was considerably higher for the former, but much closer agreement was obtained when the index for the breeding season was calculated on the assumption that for each bird seen there was another on the nest. For ordinary British habitats, its value appears to vary between 1·6 and 7·5; it was highest in mixed habitats. The variable factor of conspicuousness was not taken into account; but there is no evidence that it seriously affects the results.

3. PARASITES

Ash, J. (1950). Some Berkshire records of Siphonaptera in 1949. *Ent. Mon. Mag.* **86**, 359.

A list, with hosts, dates and sexes.

Ash, J. (1950). Records of *Ornithomya* spp. (Dipt., Hippoboscidae) from Berkshire and Co. Durham in 1949. *Ent. Mon. Mag.* **86**, 86–87.

Hosts and dates for thirteen records from Silwood Park and one from Co. Durham involving three species of *Ornithomya*, with, for each month, the total numbers of birds and the numbers of each species parasitized by each species of *Ornithomya*, and lists showing the number of adult and young birds of various species that were unparasitized.

van Emden, F. I. (1950). Dipterous parasites of Coleoptera. *Ent. Mon. Mag.* **86**, 182–206.

A parasite list, arranged to show the relation between host selection and phylogenetic relationship, giving host and parasite genera, the systematic position of the hosts, and the host stage from which each parasite usually emerges, and a host list, giving species of hosts and parasites.

Hill, A. R. (1950). An Ichneumonid (Hym.) parasite of *Lampronia rubiella* (Bjerk.) (Lep., Lamproniidae). *Ent. Mon. Mag.* **86**, 216.

Horogenes exareolatus, bred in September from a larva, is the first parasite recorded from this host.

Leatherdale, D. (1950). Notes on the degree of galling caused by *Eriophyes avellanae* Nalepa (Acarina, Eriophyidae) on hazel. *Ent. Mon. Mag.* **86**, 357–358.

In 1949, the percentages of apical buds, axillary buds and male catkins of hazel galled by *Eriophyes avellanae* in a hedgerow in Oxfordshire that had not been trimmed since 1941 were 91, 69·23 and 8·3, espectively, whereas the corresponding figures for a nearby hedge that had been trimmed since 1945 were 30, 0·7 and 0·3.

O'Mahony, E. (1950). Ectoparasites from Fair Isle. 2. *Ent. Mon. Mag.* **86**, 71.

Three Siphonaptera, four Mallophaga and one Hippoboscid, with hosts and circumstances of capture.

Spittle, R. J. (1950). Parasites of birds and mammals in the Society's area. *Middle-Thames Nat.* **3**, 31–32.

A list, with hosts, dates and localities, of Acarina, Anoplura, Aphaniptera (including two new British host records), Diptera and Hemiptera taken within an 18-mile radius of Slough.

Vickers, K. U. (1951). Some trematodes from fresh-water fish in north-east Ireland. *Irish Nat. J.* **10**, 189–190.

Records of three monogenic and four digenic species are given as well as two larval forms; all were found within 40 miles of Belfast.

Woodroffe, G. E. & Southgate, B. J. (1950). Notes on the insect fauna of birds' nests. *Middle-Thames Nat.* **3**, 28–31.

Contains a list of the bird parasites and nest scavengers and their parasites and predators found in nests of several bird species from buildings or holes in trees in the Slough area, with notes on their abundance and economic status as household pests. Includes a new county record.

4. FOOD AND FOOD HABITS

Adamson, B. (1950). Bats in the scullery. *Middle-Thames Nat.* **3**, 27.

A noctule bat (*Nyctalus noctula*) in captivity fed only on mealworms and refused blow-flies, moths and small pieces of lean meat. Four barbastelles (*Barbastella barbastellus*) took *Lucilia sericata* and mealworms, but refused *Calliphora vomitoria* and larvae and adults of the moths, *Ephestia* and *Galleria*.

Allan, P. B. M. (1951). A note on *Hyloicus pinastri* L. *Ent. Rec.* **63**, 86–87.

Observations suggesting that the horns of newly emerged larvae do not turn black until the chorion has been eaten, and that the latter contains some substance essential to the larva.

Allan, P. B. M. (1951). Moths and bats. *Ent. Rec.* **63**, 116–118.

Includes a list of Noctuids eaten by a pipistrelle bat and a discussion of the relative speeds of the bat and the moths.

Brian, M. V. & Brian, A. D. (1950). Bird predation of defoliating caterpillars. *Scot. Nat.* **62**, 88–92.

In a survey of oaks on the coast plain north of the Firth of Clyde it was concluded that the birds were having a significant effect on the population of defoliating larvae.

Cott, H. B. (1951). The palatability of the eggs of birds: illustrated by experiments on the food preferences of the hedgehog (*Erinaceus europaeus*). *Proc. Zool. Soc. Lond.* **121**, 1–42.

Twenty-five species of birds were used and the palatability of equal amounts of their shell-less eggs measured by offering a choice of two to hedgehogs; this gave consistent results. The relations between the series of palatabilities so obtained and the taxonomy, adult size, nesting habits, shell colour and a general vulnerability rating are studied and shown to vary inversely. Unpalatable eggs tend to have distinctive coloration.

Cott, H. B. (1952). The palatability of the eggs of birds: illustrated by three seasons' experiments (1947, 1948 and 1950) on the food preferences of the rat (*Rattus norvegicus*); and with special reference to the protective adaptations of eggs considered in relation to vulnerability. *Proc. Zool. Soc. Lond.* **122**, 1–54.

Palatability to the rat of eggs of forty-five species is investigated; eggs of species such as gulls and the domestic hen are greatly preferred, those of species such as the ringed plover, black cap, Great and Blue tit and linnet are avoided; thus the rat conforms in general to the reactions of man and hedgehog. Passerine eggs tend to be distasteful, otherwise there is no relation to the systematic position or feeding habits or quality of the flesh of the parents. However more palatable eggs come from larger parents, colonial species, species from inaccessible nest sites and those laying cryptically coloured eggs.

Currie, P. W. E. (1950). Records of spider prey of Pompilid and Sphecid wasps (Hym.). *Ent. Mon. Mag.* **86**, 80.

Records for four predator species.

Dunk, H. C. (1950). *Eumenis semele* at flowers. *Entomologist*, **83**, 254.

Unusual feeding by adults at flowers of bog pimpernel, pyramidal orchis, thistle, bird's-foot trefoil and dewberry in Lancashire sand-dunes.

Edwards, J. (1952). Autumn Diptera visiting fungi. *Ent. Rec.* **64**, 123–125.

Flies appeared to be more numerous on *Polystictus versicolor* than on *Russula* sp. growing on tree stumps, and counts on six occasions over a period of a month of flies on these two fungi growing on the same beech stump showed that there were twenty-nine individuals of sixteen species on the former and twenty-one individuals of fourteen species on the latter. Only Clythiids were found on another *Polystictus* on an oak stump.

Fretter, V. (1951). Some observations on the British Cypraeids. *Proc. Malac. Soc. Lond.* **29** (1), 14–20.

The four British species of Cypraeidae (Gastropoda, Mesogastropoda) feed on sessile colonial animals. *Erato voluta* and *Trivia monacha* and *T. arctica* use the proboscis to feed on compound ascidians. *Erato* thrusts its proboscis through the open mouth of a zooid of *Botryllus* or *Botrylloides* and eats the flesh, avoiding the test: *Trivia* rasps the test and feeds on the zooids within. *Simnia* eats the flesh of *Alcyonium digitatum* and *Eunicella verrucosa*.

Gauld, D. T. (1951). The grazing rate of planktonic copepods. *J. Mar. Biol. Ass. U.K.* **29**, 695–706.

Filtering rate of four species measured, and found to be independent of the concentration of the food organism (*Chlamydomonas*). Some evidence was obtained that grazing does not occur throughout the twenty-four hours.

Green, J. (1950). The feeding habits of *Cylindronotus laevioctostriatus* (Goeze) (Col., Tenebrionidae). *Ent. Mon. Mag.* **86**, 92–93.

In Epping Forest, this beetle feeds mainly during warm weather, in trees in the summer and on the ground in winter. The food was the green alga *Pleurococcus* sp., and, to some extent, associated algae. Only algae damaged during ingestion were digested.

Haggett, G. (1951). Further observations on *Zeuzera pyrina* L. *Entomologist*, **84**, 31–33.

Young larvae often make spiral galleries that may be 18 in. long immediately below the bark in the smaller stems of bushes; the pith is not, therefore, an essential food. In one wood, larval borings were confined, except in clearings, to the tree tops, where the larvae had evidently been driven as the privet and young trees on which they formerly fed became overshaded and crowded out.

Hedges, A. V. (1950). A note on the life-history of *Madopa salicalis*. *Entomologist*, **83**, 97–98.

Young larvae fed on the young leaves, extreme tip of the shoots and, where soft enough, the stems of aspen preferring the suckers. The scarcity of this Noctuid is attributed in part to the cutting back of the suckers and undergrowth each year when the young larvae are present.

odgson, S. B. (1950). Birds chasing orange underwings. *Entomologist*, **83**, 190.

A chaffinch repeatedly attacked *Brephos parthenias* and *B. notha* flying in numbers by a wood in ertfordshire in April 1950. Similar attempts by a willow-wren were seen two years previously.

odgson, S. B. (1950). A bat feeding by day. *Entomologist*, **83**, 211.

A whiskered bat (*Myotis mystacinus*) hawking gnats over water in bright sunshine at midday.

acobs, S. N. A. (1952). *Adoxophyes orana* in Kent. *Ent. Rec.* **64**, 86–87.

Records larvae of *A. orana* damaging apple at Bromley, Kent, and those of *Hoffmanophila pseudo-retella* eating apple peel where fruits stored in the dark touched the shelf.

Iaclaurin, A. M. (1951). Larva of *Lasiocampa quercus* L. race *callunae* attacked by *Carabus problematicus* (Col. Carabidae). *Ent. Rec.* **63**, 84.

Iasson, F. M. & Oxford, A. E. (1951). The action of the ciliates of the sheep's rumen upon various water-soluble carbohydrates, including polysaccharides. *J. Gen. Microbiol.* **5**, 664–672.

The physiological differences between holotrich and oligotrich ciliates are stressed. The former are elieved to utilize sugars liberated from plant material by bacteria. Competition with the bacteria is robable.

Newstead, R. (1948). Notes on the menu of little owls. *Northw. Nat.* **23**, 156–157.

The stomach contents of a male and a female *Athene noctua* chiefly comprised *Geotrupes stercorarius*, vith fragments of *Melolontha vulgaris*, *Aphodius fimetarius*, *Carabus violaceus*, earwigs, earthworms and ones of *Microtus hirtus*. Another male contained the remains of dipterous and lepidopterous larvae, earwigs, *Agriotes*, *Geotrupes stercorarius*, grass, lichens, and one of its own feathers.

Parmenter, L. (1951). Flies on the stinkhorn fungus, *Phallus impudicus* Pers. *Ent. Rec.* **63**, 59–60.

Lists showing the numbers and sexes of flies of different species taken on two stinkhorns in October 937 and November 1948, with some discussion of the seasonal relative abundance of the sexes.

Parmenter, L. (1951). Flies taken by a spider, *Dictyna uncinata* Thorell. *Ent. Rec.* **63**, 254.

A Dolichopodid, three Empids and a Sapromyzid.

Parmenter, L. (1952). Flies at ivy-bloom. *Ent. Rec.* **64**, 90–91.

A list of usual, less usual and unexpected visitors.

Platt, M. I. (1951). Diet of golden eagle. *Scot. Nat.* **63**, 67.

Castings of *Aquila chrysaëtos* from south-west Scotland showed remains of *Vulpes vulpes* (cub), *Lepus timidus*, *Corvus corone*, *Anas crecca* and *Phasianus colchicus*.

Ratcliffe, D. A. (1951). Diet of golden eagle. *Scot. Nat.* **63**, 189.

Remains of domestic fowl, rabbit and stoat found at eyrie of *Aquila chrysaëtos* in south-west Scotland.

Roebuck, A. (1951). Notes on the economic zoology of Lincolnshire during 1950. *Trans. Lincs Nat. Union*, **12**, 211–212.

Foodstuffs of various pests, mostly insects.

Smith, K. G. V. (1950). *Troilus luridus* F. (Hem., Pentatomidae) with *Coccinella septempunctata* L. (Col., Coccinellidae) as prey. *Ent. Mon. Mag.* **86**, 84.

Smyly, W. J. P. (1952). Observations on the food of the fry of perch (*Perca fluviatilis* Linn.) in Windermere. *Proc. Zool. Soc. Lond.* **122**, 407–416.

Seine nettings of fry between 1 and 6 cm. size classes were correlated with zooplankton hauls. The atter were mainly eaten, benthos only after an age of 1 month. In a single collection the fry nainly contained a single crustacean. In late summer, associated with shoaling, however, it appeared hat different shoals concentrated on different species. A July minimum of food was associated with annibalism and occurred every year at one station. Availability and abundance were correlated in some rey species, especially *Bosmina* and *Diaptomus* (which were shown in the laboratory to be easy prey), ot in others. A tendency for large fry to feed on large prey was noted.

Stroyan, H. L. G. (1950). Spiders and *Melitaea athalia*. *Entomologist*, **83**, 231–233.

In a wood where some 100–150 *M. athalia* were flying, twelve dead ones were found spun to gra spikes and partly devoured by spiders; and a further six were found on a subsequent visit. The butte flies, which were lethargic on settling, were stalked by the spiders and not trapped in webs. Man butterflies of other species were present, but were not attacked.

Todd, V. (1950). Prey of harvestmen (Arachnida, Opiliones). *Ent. Mon. Mag.* **86**, 252–25

Lists of Isopods, insects, snails and harvestmen preyed on by *Leiobunum rotundum*, *Mitopus mori Lacinius ephippiatus*, *Phalangium opilio* and *Oligolophus tridens* in a wood at night.

Walshe, B. M. (1951). The feeding habits of certain chironomid larvae (subfamily Tend pedinae). *Proc. Zool. Soc. Lond.* **121**, 63–79.

Gut contents of field specimens and feeding studies in the laboratory were combined; methods feeding vary from the use of elaborate filtering nets, to the ingestion of mud or mud-surface algae an detritus. Filter feeders may live in mud or mines in plants. Feeding activity does not vary with th amount of food caught.

5. MIGRATION, DISPERSAL AND INTRODUCTIONS

G. H. A. & R. C. (1951). Notes from Spurn, July 1951. *Naturalist*, **1951**, 176.

Among a number of observations on migration the most interesting were those which provide evidence of the eastward moult-migration of sheld-duck down the Humber from the west.

Barnes, H. (1950). *Sagitta setosa* J. Müller in the Clyde. *Nature, Lond.* **166**, 447.

This species, hitherto considered to be absent from the Clyde, has been caught there on tw occasions.

Bishop, M. W. H. (1950). Distribution of *Balanus amphitrite* Darwin var. *denticula* Broch. *Nature, Lond.* **165**, 409.

First published record in British waters, where it appears to be quite common.

Bishop, M. W. H. (1951). Distribution of barnacles by ships. *Nature, Lond.* **167**, 531.

Balanus eburneus has spread from the east coast of America to the Mediterranean, and *B. improvisu* from North temperate regions, now occurs in Australia. The role of ships in dispersing cirripedes briefly discussed.

Borland, J. F. & Walls, F. D. E. (1951). Notes on the birds of Sanda Island. *Scot. Na* **63**, 178–182.

List of birds seen in June; few details of habitat.

Bostock, H. (1950). Geese of the Mersey. *Rep. Lancs & Ches. Fauna Committee* **29** (194 75–78.

Notes on the grey goose population of the Mersey marshes.

Chang, H. W. (1951). On *Callionymus reticulatus* C. & V. and its distribution in Europe seas. *J. Mar. Biol. Ass. U.K.* **30**, 297–312.

Three species of *Callionymus* occur in British waters; *C. reticulatus* is here recognized as distin for the first time, and its distinguishing characters fully described. Some account is given of t distribution of this species at Plymouth and in European seas.

Collingwood, C. A. (1951). The distribution of ants in north-west Scotland. *Scot. Na* **63**, 45–49.

With brief notes on habitat.

Dannreuther, T. (1951). Insect immigration in 1950. *Scot. Nat.* **63**, 122–127.

Report on migrant Lepidoptera in the British Isles in 1950, a poor year for *Vanessa cardui* but a go one for *Herse convolvuli*.

Duncan, A. B. (1951). Insects collected on the Isle of Gigha. *Scot. Nat.* **63**, 184–185.

Orthoptera (1), Lepidoptera (3), Hymenoptera (8), and Diptera (8).

'orman, B. (1951). The spiders of Aberdeenshire. *Scot. Nat.* **63**, 137–155.

With notes on habitats.

'orman, B. (1951). The harvestmen (Phalangida) of Aberdeenshire. *Scot. Nat.* **63**, 156–158.

With notes on habitats.

'ryer, G. (1951). The Amphipod *Eucrangonyx gracilis* S. I. Smith) and its occurrence in Yorkshire. *Naturalist*, 65–66.

E. gracilis was first recorded on 5 July 1951 at Golcar and it has since been found to be widely istributed over a distance of at least 6 miles.
The paper includes a description and drawing of a mature female.

Gibson, J. A. (1951). The breeding distribution, population and history of the birds of Ailsa Craig. *Scot. Nat.* **63**, 73–100, 159–177.

A complete census of breeding birds of the rock in the Firth of Clyde, well known for its gannetry, letailed figures for two dozen colonies in which are given for 1936–42 and 1947–50. Detailed figures or kittiwake, guillemot, razorbill and puffin colonies are also given for 1950. The status of non-breeding species is also indicated.

Hall, D. W. (1950). A note on the distribution of the peacock butterfly *Nymphalis io* in Scotland. *Scot. Nat.* **62**, 109–110.

From 1945 to 1950 there has been a general north-easterly trend in the spread of this butterfly, and t is now well established up the west coast and in central and eastern Scotland.

Hesketh, G. E. (1951). Ringing bats in Denbighshire. *Naturalist*, **1951**, 177–181.

The experiment was started in February 1950 and this paper summarizes the results obtained up to uly 1951. The bands used, which bear a serial number and the letters, GEH, EH, GH or EGH, are similar to those used in Devonshire (see 1951, *Naturalist*, 149–157). 224 bats were marked.
R. ferrum-equinum is absent from this area, but the recovery rate of *R. hipposideros* is nearly 46 % as compared with 28 % in Devon.

Homes, R. C. (1952). The duck census in the London area, 1949–51. *Lond. Bird Rep.* **15**, 53–57.

The population trends noted during these two winters for each of nine species are discussed with reference to those observed during the two previous winters and to weather conditions.

Kevan, D. K. McE. (1950). Imported earwigs at Leith. *Scot. Nat.* **62**, 179.

Prolabia arachidis and *Anisolebis annulipes* on timber, and *Labia curvicauda* and *Spongovostox gestroi* under the bark of African mahogany.

Marshall, A. J. (1952). The condition of the interstitial and spermatogenic tissue of migratory birds on arriving in England in April and May. *Proc. Zool. Soc. Lond.* **122**, 287–295.

In most passerines spermatogenesis was achieved before arrival in Britain and the condition of the gonads was remarkably uniform over twenty-five males of 8 species. Cytological evidence indicates hat sex hormones were being secreted. The initiation and termination of migratory flight and passage song are discussed.

Matthews, G. V. T. (1951). The experimental investigation of navigation in homing pigeons. *J. Exp. Biol.* **28**, 508–535.

The ability of pigeons to orient, even when released off a training line, varies much between individuals and is inherited. Overcast skies definitely reduce this power but a simple use of a sun-time angle mechanism is excluded. Other hypotheses discounted involve: random search for landmarks, atmospheric clues, earth's magnetic field and displacement recording by a time-acceleration mechanism. A possible but unlikely navigation method is suggested. A helicopter and a radio-active flight recorder were used with moderate success.

Orton, J. H. (1950). The recent extension in the distribution of the American slippe limpet, *Crepidula fornicata*, into Lyme Bay in the English Channel. *Proc. Malac. Soc Lond.* **28**, 168–184.

C. fornicata was dredged in 1946–48 in a number of locations in Lyme Bay (the most westerly of Slapton). It is estimated that the species invaded Lyme Bay, moving west, in 1942 or 1943. Self fertilization is considered possible.

Parmenter, L. (1952). The flies of the London area. I. Conopidae. *Lond. Nat.* **31**, 25–29

County records, food plants, hosts and flight dates for twenty-one British species, with more detailed localities for the nine known from the London area.

Pennie, I. D. (1950–51). The history and distribution of the capercaillie in Scotland. *Scot. Nat.* **62**, 65–87, 157–178; **63**, 4–17.

Pennie, I. D. (1951). Supplement to the Capercaillie Report. *Scot. Nat.* **63**, 135.

A detailed account of the spread of *Tetrao urogallus* in Scotland since its reintroduction in 1837–38 with a reassessment of its status based on a widely circulated questionnaire. There is no evidence to suggest that the bird is still expanding its range, and in many areas there has been a substantial decreas in the past ten years.

Pennie, I. D. (1951). The Clo Mor bird cliffs. *Scot. Nat.* **63**, 26–32.

Notes on seven species of sea-birds breeding in north-west Sutherland.

Rees, W. J. (1950). The distribution of *Octopus vulgaris* Lamarck in British waters. *J. Mar Biol. Ass. U.K.* **29**, 361–378.

The *Octopus* population on the English side of the Channel is maintained each year by larvae driftin over from breeding centres in Brittany and the Channel Islands. Plagues of *Octopus* appear to be due t higher sea temperatures over a succession of years, ensuring better breeding conditions for a species a the northern limit of its breeding range.

Richter, R. (1951). The aquatic Coleoptera of the county of Elgin. *Scot. Nat.* **63**, 101–121.

Faunistic list with notes on habitats, and lists of water-beetles taken at eight sample habitats in th county.

Rintoul, L. J. & Baxter, E. V. (1950). Natural history notes from the Isle of Gigha *Scot. Nat.* **62**, 93–97.

A list of birds seen in June, with very brief notes on mammals and insects.

Ruttledge, R. F. (1951). Some notes on Achill birds. *Irish Nat. J.* **10**, 205–207.

Field observations on several species whose status was doubtful, with additional remarks on specie whose status has recently altered.

Ruttledge, R. F. & Williamson, K. (1952). Early arrival of white-fronted geese in Ireland *Irish Nat. J.* **10**, 263–264.

Several hundred White-fronted Geese arrived in Ireland in mid-September 1951—a month earlie than usual. In the same period a specimen of the Greenland race (*Anser albifrons flavirostris*) was sho at Fair Isle. Both occurrences are correlated with meteorological conditions exceptionally favourabl to migration from Greenland.

Sergeant, D. E. & Whidborne, R. F. (1951). Birds on Mingulay in the summer of 1949 *Scot. Nat.* **63**, 18–25.

Notes on twenty-eight species, mostly breeding, on an Outer Hebridean island.

Spooner, G. M. (1950). Notes on Plymouth marine fauna: Amphipoda. *J. Mar. Biol. Ass U.K.* **29**, 247–253.

Additional records for the Plymouth area.

Steven, G. A. (1950). (Notes on the Plymouth marine fauna): Pisces. *J. Mar. Biol. Ass. U.K.* **29**, 254–255.

Records of fishes, occasional or rare at Plymouth, recently caught in the western part of the English Channel.

Thomas, I. (1951). Colorado beetle in England, 1950. *Agriculture*, **58**, 135–139.

170 single beetles reported, of which forty-five were inland. The occurrence of twenty-four in one week of June, mostly in Kent and Sussex and several in the sea or on shore, suggested a mass flight from the continent, and was followed by nine breeding colonies (out of twenty-nine in south-east England) on potatoes in the coastal region of Kent.

Tod, K. (1951). A new and unusual locality for *Anarta cordigera* (Thunberg) (Lepidoptera). *Scot. Nat.* **63**, 33–36.

An isolated colony of the small dark yellow underwing moth on an outlying spur of the Sidlaw Hills (Angus) is the southernmost in the British Isles, at the lowest altitude (650–800 ft.) at which the species has yet been observed. The food-plant, *Vaccinium myrtillus*, is an entirely new one.

Vevers, H. G. (1950). *Ophiopsila annulosa* (M. Sars) in the Plymouth area. *J. Mar. Biol. Ass. U.K.* **29**, 81.

Confirmation that this species occurs in British waters.

Wadley, N. J. P. (1952). Black redstarts in the London area, 1950. *Lond. Bird Rep.* **15**, 43–45.

A summary of breeding, non-breeding and winter records for *Phoenicurus ochrurus* in the City and Outer London. The number of breeding pairs in the City increased to thirteen, but seven fewer young flew than in the previous year.

Wilkinson, D. H. (1950). Flight recorders. A technique for the study of bird navigation. *J. Exp. Biol.* **27**, 192–197.

A simple 'clock' to measure time bird maintains flight posture is described: it has many possible applications as an integrator or timer in ecology and micrometeorology. Weight $\frac{1}{2}$ g. or less. Bombardment of emulsion by alpha particles switched on by a steel ball acting under gravity. Tracks counted under a microscope.

Wright, A. A. (1951). The effect of wind upon the autumn movements of swallows and allied species. *Hastings & E. Sussex Nat.* **7**, 229–233.

Migration overland appears not to be affected by the direction of the wind, but oversea migration seems usually, but not always, to be against or partly against the wind.

6. REPORTS OF ORGANIZATIONS

Elder, H. F. D. (1950). Isle of May Bird Observatory and Field Station: bird report, 1948 and 1949. *Scot. Nat.* **62**, 98–108.

Lists of birds seen and ringed, with brief notes on migration.

Bryson, A. G. S. (1951). Isle of May Bird Observatory report, 1950. *Scot. Nat.* **63**, 56–63.

Selected notes on bird migrants.

Lundy Field Society (1952). *Fifth Annual Report*, 1951. (Price to non-members, 2*s.* 6*d.*; L.F.S., University College, Exeter.)

The principal zoological contribution is by L. A. Harvey on the slate shores of the island (in the Bristol Channel); notes also on bird migration.

Severn Wildfowl Trust (1952). *Fourth Annual Report*, 1950–51. (Price to non-members, 10*s.*; S.W.T., New Grounds, Slimbridge, Glos.)

Includes detailed population figures for grey geese on the Severn estuary in 1950–51, with comparative figures for each year since 1946–47; an account of the Trust's campaign for marking wild grey geese, with notes on the technique of colour-marking by Hugh Boyd.

Skokholm Bird Observatory (1951). *Report for* 1950.

Includes a paper on the factors affecting the distribution of wheatears on Skokholm by P. J. Conder, and an account of homing experiments with lesser black-backed gulls by G. V. T. Matthews; also faunistic and migration notes on mammals, birds, reptiles, Amphibia, Lepidoptera and Diptera.

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		1685 2 7
Balance—Surplus for Year		8 10 6
		£1693 13 1
Journal of Ecology:		
Costs: Printing, Paper, Blocks and Binding		
Vol. 39, no.1 (500 extra copies)		359 3 10
Vol. 39, no. 2		1244 10 11
Vol. 40, nos. 1 and 2		1935 11 10
Publishers' Commission		331 12 11
Carriage, etc.		122 2 10
Clerical assistance		52 0 0
Miscellaneous Expenses		8 5 4

BALANCE SHEET AT 31 DECEMBER 1952

Assets

	£ s. d.	£ s. d.
Cash in hand at Westminster Bank:		
Current Account	1315 9 9	
Deposit Account	100 0 0	
		1415 9 9
Post Office Savings Bank Account		3640 5 10
Expenses of Meeting paid in advance		10 8 3
Investments at Cost:		
£1200 of 3½% War Loan Stock	1230 4 1	
£700 of 3% Savings Bonds 1960/70	700 0 0	
£300 of 3% Savings Bonds 1965/75	300 0 0	
£1000 of 3% Redemption Stock 1986/96	1005 18 6	
		3236 2 7
		£8302 6 5

Note: A further Asset, not valued, is the Unsold Stock of Journals, Index Volume, and *Biological Flora* Reprints held by the Publishers for the Society.

VICTOR S. SUMMERHAYES
C. E. HUBBARD
Hon. Treasurers

Liabilities

	£ s. d.	£ s. d.
Members' Subscriptions, prepaid for 1953/57		41 7 0
Library Fund		1 5 0
Printing Accounts owing to Cambridge University Press:		
Journal of Animal Ecology, Vol. 21, no. 2 & separates	562 18 0	
Journal of Ecology (various accounts)	95 13 0	
		658 11 0
Sundry Accounts owing:		11 2 5
Journal of Ecology, Editor's expenses	5 11 3	
Journal of Ecology, Clerical assistance	14 0 0	
Journal of Animal Ecology, Editor's expenses ...	7 13 10	
		27 5 1
General Revenue Account—Surplus in hand:		
Balance at 31 December 1951	7565 7 10	
Surplus for the year 1952	8 10 6	
		7573 18 4
		£8302 6 5

Audited and found correct, and as shown by the Account Books of the Society. The Bank Balance has been verified by Bank Certificate, and also the Investments.

WM NORMAN & SONS
Chartered Accountants

120, BISHOPSGATE, E.C. 2
and
56, STATION ROAD, LOUGHTON, ESSEX.
11 *March* 1953

NOTICE TO CONTRIBUTORS

Contributors are asked to study these notes with care in order to save themselves and the editor unnecessary work in the revision of manuscripts.

1. All correspondence should be addressed: **The Editor, Journal of Animal Ecology, The Ferry House, Ambleside, Westmorland.**

2. TEXT. MSS should be typed double-spaced on one side of the paper, leaving top and left-hand margins at least an inch wide. Latin names of genera and species, **but nothing else,** should be underlined. Months of the year should be abbreviated (Jan., Feb., etc.) not indicated by figures. Text-figures are to be referred to as 'Fig. 1' etc.

The *Journal's* conventions regarding cross-headings should be followed, but they should not be used too freely, **nor should headings be underlined.** Only long papers need include a table of contents. The Royal Society's *General notes on the preparation of scientific papers* should be followed on points not mentioned here.

3. LATIN NAMES. Excepting those of British vertebrates, all Latin specific names should be followed by the authority when the name is first mentioned in the text or tables. Names must be verified either from a standard list such as Kloet and Hincks's *Check-List of British Insects* or by submitting the final MS to the experts who have supplied the identifications.

4. REFERENCES should be listed in alphabetical order at the end of the paper in the form:

Vevers, H. G. & Fisher, J. (1938). The 1938 census of gannets (*Sula bassana*) on Ailsa Craig. *J. Anim. Ecol.* **7**, 303–4.

Titles of journals should be abbreviated according to the *World List of Scientific Periodicals*, except that the English usage of capitals for adjectives should be followed. Before the MS is sent in, all references must be verified from the original sources; any reference not personally seen should be marked with an asterisk. **Nothing** except Latin names of genera and species should be underlined, nor should titles of papers or books be put in inverted commas.

5. TABLES should be set out on separate sheets and numbered in arabic numerals. So far as possible sufficient description should be included in the headings to make tables self-explanatory. The layout of tables should be kept as simple as possible; they are not printed 'boxed'.

6. TEXT-FIGURES. Drawings should be in jet-black indian ink, preferably on Bristol board. Shading must consist of lines or dots, not of half-tone washes. If the addition of mechanical stippling or hatching is required the area should be indicated by hatching lightly in blue pencil. Drawings should be arranged or grouped so that after suitable reduction a figure about 5 in. wide results.

Graphs should be drawn on paper ruled in blue or faint grey; axes and graduation marks must be drawn in indian ink.

All lettering, numerals and arrows should be shown lightly in pencil for insertion in uniform style by the blockmaker.

The author's name and the number of the figure should be written on the back of each. Legends for figures should be collected together at the end of the MS.

7. PLATES. Photographs will only be used to illustrate important points which cannot conveniently be shown in any other way. Unmounted, glossy, half-plate prints showing good detail and moderate, but not excessive, contrast, are required. They should be numbered separately from text-figures, and each print should bear on its back the number and the author's name.

8. PROOFS. Page-proofs only will be sent. They should be returned with the least possible delay, and the minimum of essential correction should be made. Authors are requested to pay particular attention to the checking of numerical matter, mathematical formulae, tables and lists of names.

9. REPRINTS. Authors are supplied with 50 reprints gratis. Additional copies may be purchased if ordered when the proofs are returned. Contributors from abroad should order when sending their MSS. Reprints are sent out about a month after publication.